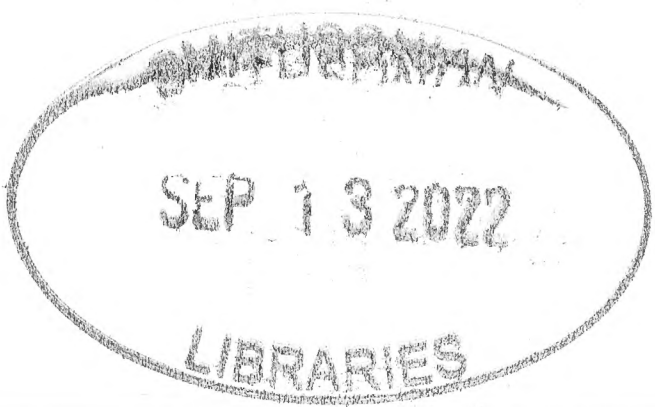




MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY



DEDICATION

VOLUME DEDICATION TO DEAN WILLIAM TAYLOR

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Editor—JUSTEN B. WHITTALL

Department of Biology
Santa Clara University
500 El Camino Real
Santa Clara, CA 95053
madronoeditor@gmail.com

Book Editor—MATT RITTER

Noteworthy Collections Editor—DAVID KEIL

Copy Editor—ALISA HOVE

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California Botanical Society
c/o Jepson Herbarium
1001 Valley Life Sciences Building
Berkeley, California 94720-2465

Administrator: Lynn Yamashita, University of California, Berkeley, CA 94720, admin@calbotsoc.org.

DEDICATION TO DEAN WILLIAM TAYLOR

September 16, 1948 – November 6, 2020

Volume 68 of Madroño is dedicated to Dr. Dean William Taylor, a friend, colleague, educator, and mentor (Fig. 1). Dean was a fixture in the California botanical community for the past 50 years and widely known for work relating to California’s rare plants, floristics, and taxonomy.

Dean was born and raised in Stockton, California. He became enamored with plants and natural history at an early age during family trips to Yosemite National Park. As a teenager, he worked summers at Silver Lake Camp near Carson Pass, Sugar Pine Point State Park at Lake Tahoe, and Sequoia National Park. It was during this time that Dean became captivated by the flora of the Sierra Nevada—the unique and rare species in the Carson Pass region held a special early fascination.

Dean’s formal education began locally, at San Joaquin Delta College; he later earned a B.S. in Biology from California State University, Fresno in 1970. Then it was off to the University of California, Davis, where he studied botany under Jack Major, Grady Webster, Michael Barbour, and Ledyard Stebbins. As a graduate student Dean lived and breathed botany—Robert Holland, a fellow student at the time, remarked upon visiting his apartment that every horizontal surface was piled with at least a foot of pressed specimens and noted the calligraphed Latin binomial labels on storage containers for his kitchen staples such as *Avena sativa* L. (oatmeal) and *Triticum aestivum* L. (flour). Ultimately, Dean earned his Ph.D. in Botany (1976) studying the ecology of the timberline vegetation at Carson Pass, Alpine County, CA.



FIG. 1. Dean W. Taylor with *Erythronium taylorii* Shevock & G.A.Allen, Tuolumne Co., CA, 2009.

From 1969 to 2020, Dean pursued, identified, and collected thousands of significant taxa deposited in California herbaria. He often jokingly referred to himself as a “modern day hay baler” of plants, and although sometimes his techniques were “somewhat unconventional” they were highly productive and valuable. He collected over 22,000 specimens, 13,800 of which are represented in the Consortium of California Herbaria (Fig. 2). While the majority of his collections were made in California, his specimens span much of North America, from Alaska to Baja California, Mexico. Dean’s collections led him and coauthors to describe five new taxa (Fig. 3) and 41 new combinations. Two new taxa were collected by Dean and described by others, both of which share the *taylorii* specific epithet (Fig. 3).

Dean authored or co-authored numerous publications: peer reviewed journal articles, technical reports, notes, and a technical flora of the Yosemite region. He was well-regarded for his many theories involving historical biogeography, intriguing plant distributions, and relict plant populations. While some of his creative floristic analyses and hypotheses are included in his published works, many more live on in projects in which he assisted or influenced,

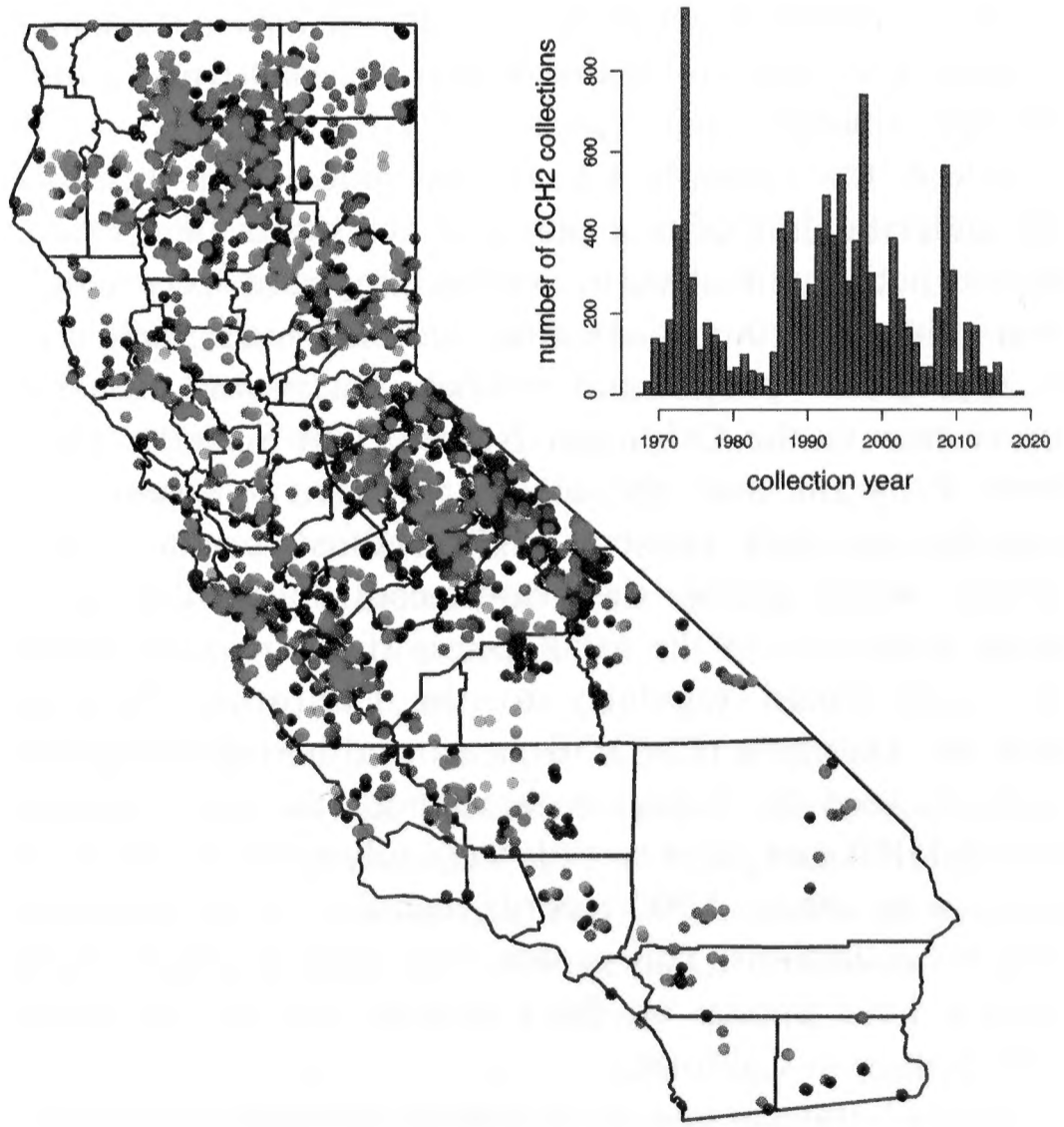


FIG. 2. Collection locations of Dean’s specimens across California represented by black and red circles, darker colors indicate multiple collections; red indicates special status taxa following criteria from the California National Diversity Database. The histogram represents collection effort over time. Data is from the Consortium of California Herbaria data portal.

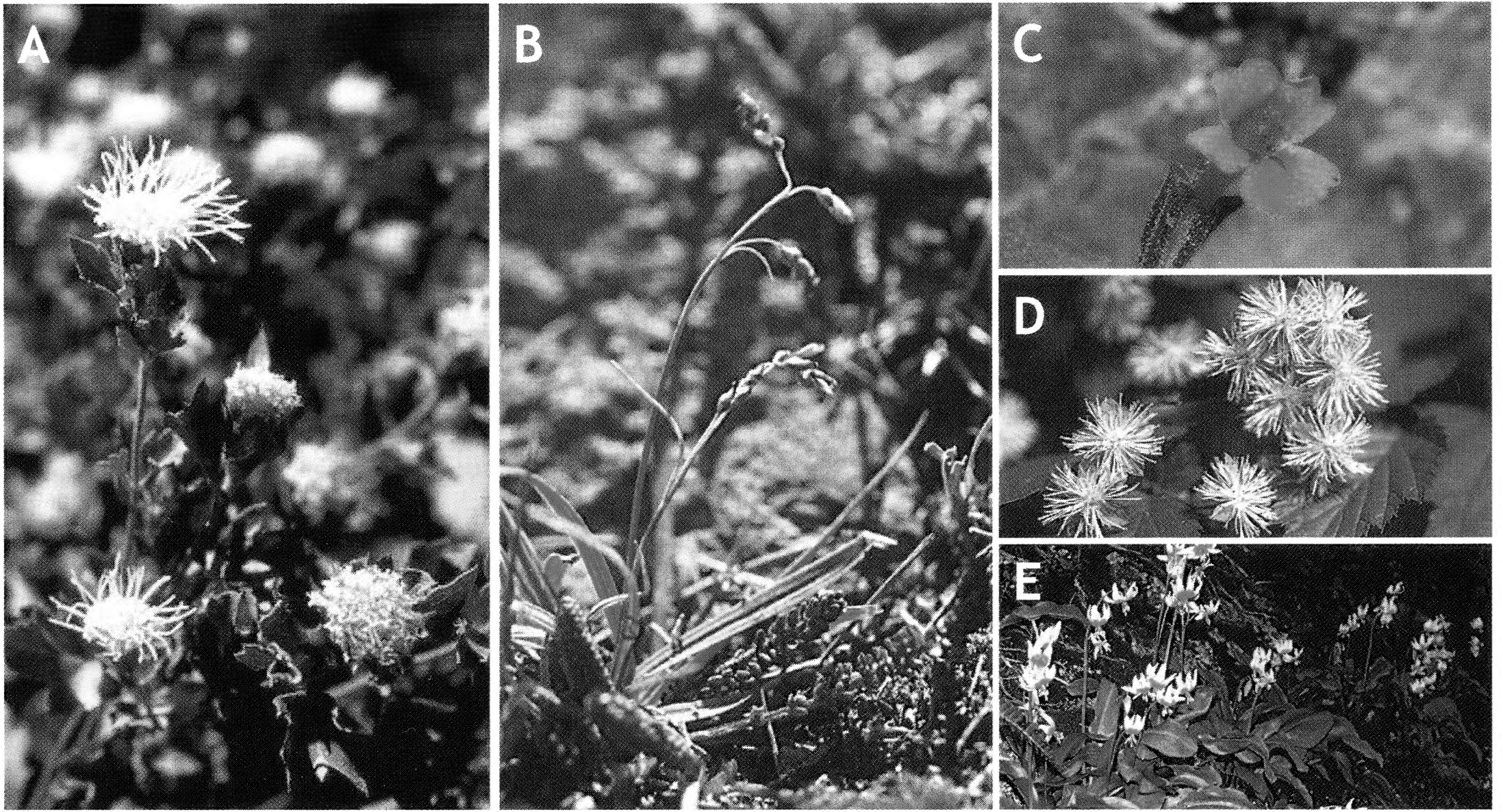


FIG. 3. Several of the many taxa Dean contributed to discovering. Photos were taken by Dean and archived on CalPhotos, where he contributed more than 2,700 images: A) *Ageratina shastensis* (D.W.Taylor & Stebbins) R.M.King & H.Rob.; B) *Carex tiogana* D.W.Taylor & J.D.Mastrog.; C) *Erythranthe taylorii* G.L.Nesom; D) *Neviusia cliftonii* Shevock, Ertter & D.W.Taylor; E) *Erythronium taylorii* Shevock & G.A.Allen.

and in work that is published or in progress by others. Dean was an effective botanical influencer; he called, texted, and sent detailed emails to botanists across the state about interesting plants or range extensions that he thought warranted attention. Countless new friendships and alliances began this way, and many memorable field trips ensued that led to further discoveries.

Indeed, few individuals have contributed more towards our understanding of rare plants in California than Dean. He was actively involved in documenting rare species and, even more importantly, assuring that data made their way to appropriate people and entities. Dean was a major contributor to the California Native Plant Society's Rare Plant Program and the associated review forum—his contributions were constant and steadfast, totaling 400+ reviews, nearly double the nearest contributor, and comprised over 80% of the total species status reviews. Dean also contributed regularly to the California Natural Diversity Database (CNDDDB), a natural heritage program routinely used by biologists throughout the state. Nearly 500 CNDDDB rare plant records were submitted by Dean, in addition to almost 1,500 records included in the database from his collections. This prolific rare plant documentation made a huge impact on the CNDDDB and to rare plant conservation in California.

Dean's botanical interests extended throughout the state, but it was in northern California that he and colleague Glenn Clifton had what Dean considered his greatest plant discovery. In May 1992, while returning home on Highway 299 east of Redding, Dean and Glenn stopped at a limestone outcrop that had piqued their interest for some time, and it was there they found what became Shasta snowwreath (*Neviusia cliftonii*) Shevock, Ertter & D.W.Taylor

(Fig. 3). This discovery was so unusual and remarkable that it even made the *New York Times*; that news clip would be proudly shown in many of Dean's *Neviusia*-related presentations.

An important part of Dean's legacy was his mentorship of budding and established botanists alike. Dean believed in building the next generation of botanists, influencing many towards additional work experience and advanced degrees. He was generous in this role. For example, when Santa Cruz botanist Randy Morgan was battling cancer and attempting to complete his *Trifolium* treatment, Dean edited, photographed, and drove him to the Jepson Herbarium on volunteer days to conduct his research. While updating the Santa Cruz County checklist as a fledgling botanist, Dylan Neubauer received tremendous help from Dean. He sent her information on his new local finds, especially novel roadside weeds from the long, wooded, winding road to his home in Aptos, California, considered by some to be the most thoroughly botanized road on the planet. As a mentor, Dean challenged people to regard the future of California's flora, and many recall his exhortations to collect, emphasizing that without a voucher, a record is less credible (or not credible).

Dean's students and colleagues recall his ardent love of botany, his broad floristic knowledge, and field trips where he would know every species encountered. Whether as a guest lecturer, co-worker, mentor, or consultant, Dean was always teaching. If someone strayed too far ahead, thus missing something along the trail, they might be recalled with a shout: "Botany Emergency!" His vehicles served as mobile botany labs, the most famous of which was the Volkswagen Bus that averaged 25,000 miles annually while conducting botany excursions. Using the Volkswagen as

backdrop during his many presentations, Dean would describe exploring remote locations and emphasize there were many more botanical discoveries left in California. He inspired many to collect in under-collected areas of the state. In later years, his mobile botany lab operated from 4WD Toyota pickups with license plates reading: "BOTNST."

Dean's early interest in montane flora developed into a lifelong passion for alpine plant communities: the Sierra Nevada, White Mountains, and Mount Shasta regions became the areas of his greatest interest and expertise (along with his home county of Santa Cruz). He had a special talent for montane *Carex* and was respected especially for fearless parsing of Section Ovals.

Dean worked in the Sierra Nevada for five decades, acting as a private consultant in the National Forests, gathering data for his flora, and making significant contributions to regional knowledge. Especially noteworthy were discoveries of new taxa such as *Erythronium taylorii* Shevock & G.A.Allen (Figs. 1, 3) and *Platanthera yosemitensis* Colwell, Sheviak, & P.E.Moore. In recent decades, Dean returned as a consulting botanist to Yosemite, participating in inventory projects there between 2003 and 2012. During this time, he completed and published his long-awaited technical *Flora of the Yosemite Sierra* (2011, Lulu Press, Morrisville, NC), or as he referred to it: "Dean's Data Download" (Fig. 4). He was planning fieldwork for a second edition with Hannah Kang this coming year.

Dean played an important role in bringing science to industry while serving as a consulting botanist for 20+ years at Sierra Pacific Industries (SPI), a company managing 1.8 million acres of private timberlands in California. In 2000, Dean partnered with SPI to start a rare plant survey program. It became the foundation of the scientifically-based SPI Botany Program and Policy, which promotes the understanding of the company's botanical resources and guides protection of endangered, threatened, and rare plants during management activities. Dean emphasized that each rare plant occurrence added valuable knowledge about these species, resulting in better forest management practices. Consequently, botanical surveys on SPI lands have identified over 2,000 plant taxa, and Dean helped develop protective measures for over 200 special status species found during those efforts. Dean stressed contributing to the CNDDDB, and SPI has submitted approximately 4,500 records as a result. Dean also initiated a publicly available herbarium for SPI, making it the first industrial forest company in California to become registered with the Index Herbariorum and to join the North American Network of Small Herbaria and Consortium of California Herbaria.

Dean's botanical legacy will continue through the actions of the hundreds of botanists he influenced and inspired, and in his thousands of collections. His passing is a huge loss to the botanical community and for those who worked and



FIG. 4. Dean checking his draft flora at Crescent Lake in Yosemite, 2009. Shortly after, Dean published his technical *Flora of the Yosemite Sierra* (2011, Lulu Press, Morrisville, NC).

interacted with Dean. He will be missed by many who enjoyed his friendship, intellect, passion for botany, guidance, and humor; including his characteristic "laughter-snort."

—JOANNA CLINES, Sierra National Forest, North Fork, CA 93643; ALISON E. COLWELL, Center for Plant Diversity, University of California, Davis, CA 95616; BARBARA ERTTER, Western North American Flora, University Herbarium and Jepson Herbarium, University of California, Berkeley, CA 94720; DENA GROSSENBACHER, Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407; LINNEA HANSON, Plumas National Forest (retired), Chico, CA 95973; ROBERT F. HOLLAND, The Nature Conservancy (retired), Auburn, CA 95603; CAJUN E. JAMES, SPI, Forestry Division, Research and Monitoring Director, Sierra Pacific Industries, Anderson, CA 96007; HANNAH KANG, ECORP Consulting, Rocklin, CA 95677; MARLA KNIGHT, Klamath National Forest (retired), Fort Jones, CA 96032; KRISTI LAZAR, California Natural Diversity Database, California Department of Fish and Wildlife, Sacramento, CA 95811; LEN LINDSTRAND III, SPI, Forestry Division, Botany Program Manager, Sierra Pacific Industries, Anderson, CA 96007; DYLAN NEUBAUER, Kenneth Norris Museum of Natural History, University of California, Santa Cruz, CA 95064; JIM SHEVOCK, California Academy of Sciences, San Francisco, CA 94118; AARON E. SIMS, California Native Plant Society, Sacramento, CA 95816; JOHN STEBBINS, California State University, Fresno (retired), Napa, CA 94558; JOHN WEHAUSEN, University of California, White Mountain Research center (retired), Bishop, CA 93514; JENN YOST, Hoover Herbarium, Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407.

NOTEWORTHY COLLECTIONS

CALIFORNIA

CASTILLEJA ANGUSTIFOLIA (NUTT.) G.DON VAR. *FLAVESCENS* (PENNEL EX EDWIN) N.H.HOLMGREN (OROBANCHACEAE). —Lassen Co., Great Basin, near the southeast corner of the Warner Mountains, along the west side of Tuledad Road about 3 air miles northeast of Dodge Reservoir and 0.5 road miles south of the west end of Tuledad Canyon, 41.018417, -120.098056 (WGS84), 1661m, on a gentle northeast-facing slope, in a flattish rocky open area with scattered junipers, many of which had been cut and piled, dominated by low sagebrush, plants abundant in this spot, inflorescence bracts a pale red-orange in some plants, pale yellow in others, and occasionally pale ivory, in medium-brown soft dry soil, among grasses and shrubs, with *Blepharipappus scaber* Hook. and scattered *Eriophyllum lanatum* (Pursh) J.Forbes var. *achilleoides* (DC.) Jeps., 5 June 2015, B. Castro 2094 with L.P. Janeway (CHCS115227), this collection annotated by J. Mark Egger, University of Washington, co-author of the *Castilleja* treatment in the Flora of North America (Egger et al. 2019); in the Consortium of California Herbaria 2 (CCH2) the image of this herbarium specimen was apparently made before the specimen was annotated, so the image does not show the annotation label, and the collection is listed in CCH2 under *Castilleja chromosa* A.Nelson.

Mono Co., Bodie Hills, northwest base of Masonic Mountain, above Forest Service Road 046, 8.5 km northeast of its intersection with CA State Hwy 182, 38.35536111, -119.14916667 (WGS84), 2491m, a perennial herb, stems erect and usually unbranched, inflorescence bract color varying in the population (but consistent within each individual) from pale yellow to dark yellow to pale orange to dark orange, but never red, this population dense, with thousands of individuals, tapestry-like in appearance, covering several acres (Fig. 1), in reddish clay overlain with volcanic gravel, with *Artemisia arbuscula* Nutt., *Lupinus nevadensis* A.Heller, *Lupinus arbustus* Dougl., *Penstemon humilis* A.Gray, *Stenotus acaulis* (Nutt.) Nutt., *Crepis occidentalis* Nutt., *Allium anceps* Kellogg, *Cusickiella quadricostata* (Rollins) Rollins, other perennial and annual herbs, and scattered *Pinus monophylla* Torr. & Frém., 28 May 2018, Ann Howald 4549 (UCR), and 11 July 2018, Ann Howald 4707 (UCR), both collections annotated by J. Mark Egger, 23 June 2019, Ann Howald 5032, 5033, 5034 (CAS); Bodie Hills, Bodie Ranch vicinity, Bodie-Fletcher Road, about 5.5 road miles northeast of its intersection with Geiger Grade (at Bodie town), 38.252278, -118.968917, (WGS84), 2377 m (this location about 18.5 km east-southeast of the Masonic Mountain

population), a multi-stemmed perennial herb, inflorescence bracts light pink-light yellow to dark yellow to light orange in this local population of about 200 individuals, on a moderately steep south-facing slope, gravelly-silty soil, with *Juniperus osteosperma* (Torr.) Little, *Artemisia arbuscula* Nutt., *Astragalus oophorus* S.Watson var. *lavinii* Barneby, *Penstemon humilis* A.Gray, other perennial and annual herbs, 2 July 2018, Ann Howald 4640, 4642, 4644, 4646 (UCR), these annotated by J. Mark Egger, 27 June 2019, Ann Howald 5039, 5043, 5045, 5046 (CAS); Bodie Hills, north of Bodie Bluff, Bodie-Fletcher Road, about 1.4 road miles northeast of its intersection with Geiger Grade (at Bodie town), 38.22675, -118.996472, (WSG84), 2525m (this location about 19 km southeast of the Masonic Mountain population), a perennial herb, bracts ranging from light yellow to dark orange in this local population of about 75 individuals, on a steep south-facing slope, sandy-silty soil with reddish-brown volcanic gravel, with *Artemisia arbuscula* Nutt., *Phlox stansburyi* (Torr.) A.Heller, *Eriogonum umbellatum* Torr. var. *nevadense* Gand., *Astragalus iodanthus* S.Watson, *Astragalus curvicaupus* (A.Heller) Macbr., other annual and perennial herbs, 27 June 2019, Ann Howald 5048 (CAS).

Previous Knowledge. Cronquist et al. (1984) describe the distribution as “Cassia County, Idaho, south in west Utah to Millard County and in eastern Nevada to White Pine County.” Egger et al. (2019) give the distribution as Nevada, Idaho and Utah, with a note stating “Recent collections from extreme eastern Mono and Modoc counties suggest that var. *flavescens* may also occur in California, but the



FIG. 1. Multi-colored population of *Castilleja angustifolia* var. *flavescens* at the northwest base of Masonic Mountain, Bodie Hills, CA.

identity of these populations has yet to be fully verified.”

Significance. These are the first reports for California. The Lassen County location is a western range extension of about 350 km from the nearest known locality, in northern Nevada, Elko County, near Hutch Creek, southwest of Pennsylvania Hill (*J. Hodzic 2017-29 RENO*), and the Bodie Hills populations represent a western range extension of about 220 km from the nearest known locality in central Nevada, Nye County, in Monitor Valley (*R.G. Swinney 777 UCR*). J. Mark Egger reports that photos exist of plants resembling *Castilleja angustifolia* var. *flavescens* from eastern Modoc County, but its presence in this area has not been verified.

—ANN M. HOWALD, 210 Chestnut Avenue, Sonoma, CA 95476, annhowald@vom.com.

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NOTEWORTHY COLLECTIONS

CALIFORNIA

DITTRICHIA VISCOSA (L.) Greuter (ASTERACEAE). —San Francisco Co., San Francisco, Hunters Point Shipyard, Hussey Street and H Street in the vicinity of Manseau Street; short, many-branched shrub, plants mostly gone to seed, but with occasional fresh heads. Could be more widespread, but most of the vicinity is publicly inaccessible. In disturbed areas (gravel, hardscape cracks), 37.721031°, -122.366664°, 3 m, 17 November 2019, *S. Batiuk 186* (CAS); Hunters Point Naval Shipyard, H Street between Spear Ave and Manseau Street; scattered, shrub to subshrub, many-branched from base, corollas yellow; flowering/fruiting; could be more widespread, but most of vicinity is publicly inaccessible. In hardscape cracks and ruderal areas, 37.722277°, -122.368956°, 3 m, 4 October 2020, *S. Batiuk 234* (CDA).

Previous knowledge. *Dittrichia viscosa* is native to the Mediterranean basin (Rosatti 2014). It was collected on the east coast of the United States in the late 1800s in ship ballast (Preston 2006), but it was not collected again in North America until 2014 in the City of Fairfield, Solano County, California (Akulova-Barlow 2015; Rosatti 2014).

Significance. These are the first collections for San Francisco City and County and the second known locality for California. The San Francisco population

is located approximately 55 km south-southwest of the Solano County population, and the method of introduction to San Francisco is unknown. The full extent of the San Francisco population is also unknown because most of the Hunters Point Shipyard is closed to public access, but given the affinity of *Dittrichia viscosa* for disturbed areas, there is high potential for it to be more widespread than what was observed by the author.

—SCOTT BATIUK, WRA, Inc., 2169-G East Francisco Blvd, San Rafael, CA 94901, batiuk@wra-ca.com.

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NOTEWORTHY COLLECTION

WASHINGTON

TARAXACUM ALASKANUM Rydb. (ASTERACEAE). —Skagit Co., Mt. Baker-Snoqualmie National Forest, Glacier Peak Wilderness, South Ridge of Magic Mountain, 48.445278°, -121.041389°, 2200 m, 29 July 2019, *Matt Below 31* (WTU). Plants growing on or near the top of the south ridge, as well as on the summit block. Four individuals were located. Growing in both thin lithosols and from bare rock. Yellow flowers, 1–2 stems per plant, taprooted. Associated species: *Luetkea pectinata* (Pursh) Kuntze, *Poa alpina* S.Watson, *Cardamine bellidifolia* All., *Veronica cusickii* A.Gray, *Anemone* sp. Geneve; Mt. Baker-Snoqualmie National Forest, Glacier Peak Wilderness, notch in ridgeline, SE of Mixup Peak, 48.451667°, -121.056944°, 2000 m, 24 August 2019, *Matt Below 36* (WTU). Individual growing from lithosols on a ledge in a shaded, N-facing gully. Lone plant in seed. Cypselae grayish brown. Associated species: *Cerastium beeringianum* Cham. & Schltdl., *Saxifraga cespitosa* L., *Veronica cusickii*, *Poa alpina*, *Trisetum spicatum* (L.) K.Richt.

Previous knowledge. According to the Consortium of Pacific Northwest Herbaria (2020), populations of *Taraxacum alaskanum* have been documented in British Columbia, Yukon, Alaska, and Eastern Russia. Plants can be found growing in arctic tundra, alpine slopes and tundra, and seaside bluffs (Brouillet 2006).

Significance. These are the first collections of *T. alaskanum* in Washington and represent a range extension approximately 73 km southwest of the nearest population in the Cascade Range at Manning Park, British Columbia, Canada. Due to the rugged terrain and challenging access, this area of the North Cascades is sparsely surveyed. Consequently, further surveys in the area could lead to the discovery of additional populations, potentially further south into the range. Given the location of this population, future monitoring of these populations could prove to be advantageous for studying the effects of climate change on alpine plant communities.

TARAXACUM SCOPULORUM (A.Gray) Rydb. (ASTERACEAE). —Whatcom Co., Mt. Baker, Skyline Ridge, 1828 m, on open alpine crest, 11 July 1934, *J. William Thompson 11006*.

Previous knowledge. According to the Flora of North America treatment (Brouillet 2006) *T. scopulorum* ranges from Northwest Territory south to British Columbia, Idaho, and Montana, and eastward across northern Canada to Greenland. The

habitat for southern populations of this species is alpine tundra. J. William Thompson did not assign a species name to his 1934 collection (11006) of *Taraxacum* from Mt. Baker. In 1985, an unknown researcher at WTU annotated the specimen as *T. scopulorum* and placed the annotation slip in the specimen fragment folder, thus obscuring it from view. The specimen was then errantly filed under *T. lyrata*, a mistake that was not discovered until 2019, at which time the 1985 *T. scopulorum* determination was confirmed.

Significance. This is the first and only record of this species in Washington and represents the southern- and westernmost documented locality for the species. The Consortium of Pacific Northwest Herbaria (2020) database shows the closest documented populations are in southcentral British Columbia and northwestern Idaho, though these specimens have not been examined by the authors. R. L. Taylor made extensive botanical surveys of the Mt. Baker alpine zone from the 1960's to the 1980's but did not collect this species, so the status of this historic population remains uncertain.

BOECHERA CASCADENSIS Windham & Al-Shehbaz (BRASSICACEAE). —Yakima Co., Okanogan-Wenatchee National Forest. Chimney Peaks, approximately 5 km in on Forest Service Road 1200 from Tieton Road., 46.64864°, -121.0793° (datum: WGS 84; coordinate uncertainty: 50 m; coordinate source: digital map), 1150 m, 18 June 2014m, *David Giblin 5275* (WTU). Rock outcropping of apparent volcanic origin; soil very thin and almost ashy. *Eriogonum compositum* Douglas ex. Benth., *Erigeron linearis* Spreng. ex DC., *Heuchera cylindrica* Douglas, and *Saxifraga bronchialis* L. common. Low, dense mats from a central taproot; fruits arcuate.

Previous knowledge. *Boechea cascadiensis*, an apomictic triploid of putative *B. paupercula* (Greene) Windham & Al-Shehbaz and *B. microphylla* (Nutt.) Dorn parentage, is known only from the holotype locality in Kittitas Co., Washington and possibly from a site in Baker County, OR (Windham & Al-Shehbaz 2007). *Boechea paupercula* has been documented twice in Washington's Olympic Mountains, a distance of over 300 km to the west of the two *B. cascadiensis* sites. *Boechea microphylla* is widely distributed in Washington's East Cascades region, and is well-documented in general proximity to the historic and contemporary *B. cascadiensis* sites.

Significance. *Boechea cascadiensis* is a narrow endemic listed as potentially extirpated in Washing-

ton. *Boechea paupercula* is on Washington's Review List as a potentially extirpated disjunct, known from only two historic (1934) localities in the Olympic Mountains (Washington Natural Heritage Program 2019). Hybridization, polyploidy, and apomixis in *Boechea* is well known and creates significant challenges to accurate determinations. It is possible that additional populations of both these species exist in Kittitas and Yakima counties.

—MATT BELOW, Seattle, WA, bluebusrider@gmail.com; and DAVID E. GIBLIN, University of Washington Herbarium, Burke Museum of Natural History and Culture, Box 355325, Seattle, WA 98195-5325.

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WOODY VEGETATION ENCROACHMENT: A DRIVER OF HERBACEOUS SPECIES DIVERSITY LOSS IN A COASTAL FEN

J. L. SALER AND E. S. JULES

Department of Biological Sciences, Humboldt State University, 1 Harpst Street,
Arcata, CA 95521
jls1011@humboldt.edu

ABSTRACT

Early successional wetland habitat is being lost in temperate regions worldwide as a result of changes in disturbance regimes that allow for the establishment and dominance of woody species. This phenomenon is pronounced in fens, which harbor high numbers of special status plant species that require early successional habitat. We investigated the relationship between woody vegetation encroachment and herbaceous species richness within a northern California coastal fen that has been undergoing encroachment by woody vegetation for ca. 80 years. We established 25 transects within the fen and sampled 338 1x1 m plots located at 4-m intervals along transects. At each plot, we recorded the cover of all woody and herbaceous species, as well as litter, thatch, open water, bare soil, and cover of large woody debris. Modeling indicated that woody vegetation cover, height, species richness, litter cover, and distance from the edge of fen were significant predictors of herbaceous species richness. Vegetation sampling indicated that herbaceous species richness declined with increased woody vegetation cover and height and increased litter cover. Canopy closure was found to result in the complete loss of rare plant species and a significant reduction in herbaceous species richness. The results of this study suggest that the re-introduction of disturbance, specifically those that result in the removal of woody vegetation and litter accumulation, is probably essential to maintain herbaceous species diversity and persistence of special status plant species populations in coastal fens.

Key Words: encroachment, fen, plant diversity, rare plants, succession, wetlands.

INTRODUCTION

Wetlands are among the most threatened ecosystems in the world, with half of global wetland area having been lost over the last two centuries (Duffy and Kahara 2011; Davidson 2014; Van Meter and Basu 2015). The loss of wetlands has been most concentrated in temperate regions, where industrialization, transportation projects, and agricultural development have been particularly intensive (Tiner 1984; Armentano and Menges 1986; Turner 1991; Mattingly 1994; Gibbs 2000; Brinson and Malváres 2002; Gutzwiller and Flather 2011). For example, portions of southern and eastern Europe, the southeastern United States, and California have lost an estimated 90% of their wetlands primarily in the last 150 years (Hefner and Brown 1984; Dahl and Alford 2004; Finlayson and Spiers 1999; Dark et al. 2006). Loss of habitat has resulted in a loss of species diversity from these regions (Euliss et al. 1999; Brinson and Malváres 2002; Duffy and Kahara 2011; Van Meter and Basu 2015). To a lesser (yet increasing) extent, wetlands have also been lost or severely degraded due to changes in disturbance regimes, in particular changes in grazing patterns, fire return intervals and fire behavior. These changes can result in the loss of wetland habitat, particularly in areas such as California, the southeastern United States, and central Europe (Hobbs and Hueneker 1992; Güsewell and Le Nédec 2004; Martin and Kirkman 2009).

In response to historical and on-going loss of wetland habitat, many wetland areas within North America and Europe have been set aside for conservation through land purchases and increased regulatory protection (Dahl 2006; Duffy and Kahara 2011). Physical disturbance as a form of conservation management, including timber harvest and livestock grazing, is usually excluded from protected wetlands. More importantly, fire exclusion, especially within the vicinity of populated areas, has impacted the natural disturbance regimes of many wetland ecosystems within the state of California (Hobbs and Hueneker 1992; Bowles et al. 1996). Disturbance is an important component of many ecosystems, and many plant communities are entirely dependent on some disturbances (Pickett and White 1985). In the absence of disturbance many wetland systems become increasingly dominated by woody vegetation (Godwin et al. 1974; Christy 1979; Bowles et al. 1996; Güsewell and Le Nédec 2004; Middleton et al. 2006; Warren et al. 2007). Woody vegetation encroachment and the associated transition towards drier soils is occurring in many wetland types, resulting in a marked decline in herbaceous species richness and cover (Bowles et al. 1996; Güsewell and Le Nédec 2004; Middleton et al. 2006; Taft and Kron 2014; Taylor et al. 2018). Many special status wetland plant species are dependent on early successional conditions, and as such are increasingly at risk of extirpation from protected wetlands that are without appropriate natural or managed disturbance (Gibbs 2000; Van Meter and Basu 2015). For example,

wetlands in the southern Appalachian Mountains, which harbor a disproportionate number of special status plant species, are currently being impacted by woody vegetation encroachment and dominance (Warren et al. 2007), and herbaceous dominated wetlands in Switzerland, previously used for grazing, have been observed to be losing herbaceous species diversity following a cessation of agricultural use (Matthias et al. 2001; Güsewell and Le Nédec 2004). The loss of habitat dominated by herbaceous species within protected wetlands is of particular concern, as these areas were set aside as refugia for wetland dependent species in the face of historic wetland loss (Johnston et al. 2007).

Woody vegetation encroachment is more pronounced in fen wetlands as compared to other wetland types such as bogs (Johnson 1996; Van den Broek and Beltman 2006). Fens and bogs are described as peatlands (i.e., sites where plant growth exceeds decomposition). Bog soils are highly acidic and have nutrient poor peat, whereas fens have nutrient-rich, slightly acidic, neutral to even alkaline mineralized organic soils as a result of through-flowing water. These characteristics make fens species rich, productive, and subject to rapid organic matter accumulation and hydrologic change (Baker 1972; Erman et al. 1977; Leppig 2004; Weixelman and Cooper 2009; Granath et al. 2010). Fens are recognized as being early successional wetlands (Gorham and Rochefort 2003; Baker 1972) and support early successional plant communities. In the absence of disturbance, however, the rapid plant growth, high sediment input, and minimal decomposition of organic material allows for aggressive growth of woody vegetation (Wilson and Keddy 1986; Hausman et al. 2007; Johnston 2009). In several studies, repeated disturbance was necessary to prevent fens from transitioning to drier systems dominated by woody species. Fire was found to maintain prairie fen diversity (Bowles et al. 1996) and mowing of Swiss fens every three years was found to maintain or increase herbaceous species diversity (Güsewell and Le Nédec 2004).

Fen habitat is relatively uncommon in California, where it primarily occurs at higher elevations (Leppig 2004; Sikes et al. 2013). At lower elevations, fens are known from locations along the Pacific Coast of northern California (Baker 1972; Leppig 2002), with additional fens along the immediate coast north of California (Christy 1979). Because of their uncommon distribution, fens are known to harbor a high diversity of uncommon special status plant species and sensitive natural communities (Rubtzoff 1953; Baker 1972; Barry and Schlinger 1977; Christy 1979; Leppig 2002; Leppig 2004; Bencie and Kalt 2007).

Big Lagoon Bog is a fen along the north coast of California and represents an uncommon habitat that supports numerous special status plant species (Leppig 2002; Leppig 2004; Smith 2014). A total of 90 plant species have been recorded from Big Lagoon Bog prior to this study (Leppig 2002; Smith 2014). Of

the 90 species recorded, 11 are considered rare in California, representing approximately 12% of the species diversity present within the fen. Of the 11 special status plant species reported from Big Lagoon Bog, *Juncus nevadensis* var. *inventus* (L.F.Hend.) C.L.Hitchc. (dune rush, Juncaceae) and *Vaccinium uliginosum* var. *occidentale* (A.Gray) Hulten (western blueberry, Ericaceae) are presumed to be extirpated from the site. *Carex leptalea* Wahlenb. (bristle-stalked sedge, Cyperaceae) has not been observed since 2012 and its continued existence at this site is unknown, and another species, *Lycopodiella inundata* (L.) Holub (inundated bog club-moss, Lycopodiaceae), is in immediate risk of extirpation. *Lycopodiella inundata* is a circumboreal species known from two locations in the state of California (CNDDDB 2019). The population of *L. inundata* within Big Lagoon Bog has been slowly decreasing, and now consists of a few individuals in a single location within the fen (Gordon Leppig, pers. comm.). *Viola pulustris* L. (alpine marsh violet, Violaceae), *Drosera rotundifolia* L. (round-leaved sundew, Droseraceae), and *Carex buxbaumii* Wahlenb. (Buxbaum's sedge, Cyperaceae) are wetland dependent species restricted to coastal or montane wetlands in California (Baldwin et al. 2012). Sphagnum moss is known from only a few disparate locations along the coast of California (CNDDDB 2019). In fact, many of the special status plant populations recorded from Big Lagoon Bog are isolated peripheral populations (Leppig 2002; Leppig 2004; CNDDDB 2019) and therefore likely possess distinct genetic and ecological characteristics (Leppig and White 2006) making their preservation all the more urgent. All of the special status plant species reported from Big Lagoon Bog require early successional open habitat (Baldwin et al. 2012).

A marked and progressive decline in open habitat within Big Lagoon Bog has been documented due to encroachment by woody vegetation for at least the last four decades (Christy 1979; Leppig 2004; Bencie and Kalt 2007). It is estimated that 60% of the open early successional habitat in Big Lagoon Bog has been lost as a result of woody vegetation encroachment (Dave Imper, United States Fish and Wildlife Service, personal communication). A progressively faster rate of woody vegetation encroachment has been observed within Big Lagoon Bog and in other similar habitats throughout the surrounding region (Christy 1979; Leppig 2002; Bencie and Kalt 2007). Many similar fens along the coast have been eliminated in the last 10–20 years due to woody vegetation encroachment and progression to forested habitat (Christy 1979; Bencie and Kalt 2007). Of the 19 fens along the Pacific Coast studied by Christy in 1979, 15 were experiencing invasion by woody vegetation, and open, early successional habitat was found to be disappearing as a whole (Christy 1979).

Within Big Lagoon Bog the dramatic increase in woody vegetation is directly linked to a cessation of disturbance. Historically the area may have experi-

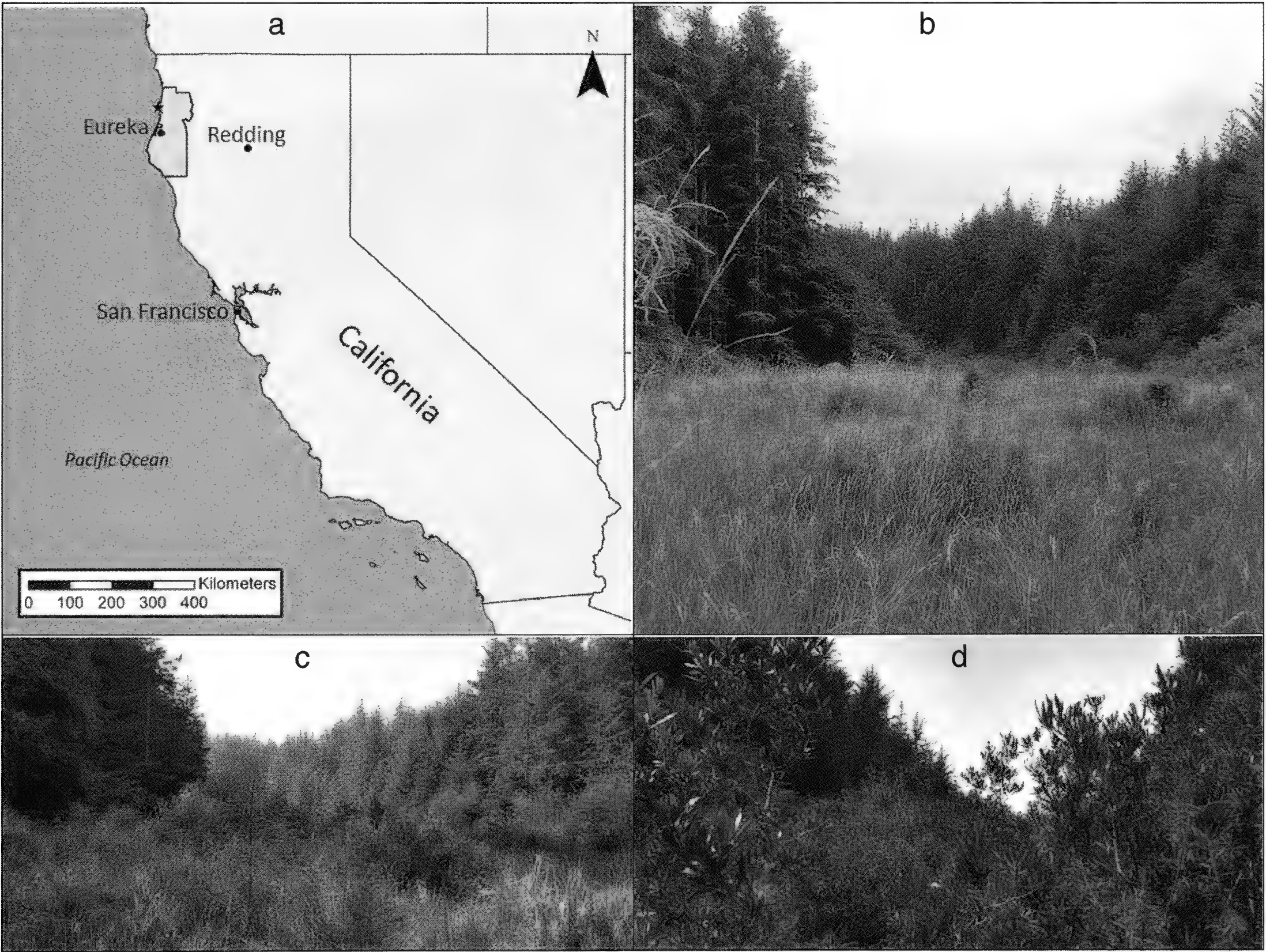


FIG. 1. Study location of Big Lagoon Bog in Humboldt County, California as denoted by the star (Panel a). Looking south across the open center of Big Lagoon Bog (Panel b), looking south within Big Lagoon Bog showing moderate to low woody vegetation cover (Panel c), Big Lagoon Bog looking north with nearly complete woody vegetation canopy closure (Panel d).

enced natural and human-caused fire events, and large elk herds and beaver may have provided a check on woody vegetation growth. In addition, tsunami events have been recorded from the area which would have greatly impacted Big Lagoon Bog as evidenced by tsunami sediment deposits (Gordon Leppig, Humboldt State University, personal communication). The area was grazed and surrounding lands were farmed in the late 1800's. Grazing ceased in the late 1930's or early 1940's with the construction of nearby vacation homes, and this appears to be linked with the establishment of woody vegetation (Don Tuttle, Board President of the Big Lagoon Park Company, personal communication). Lastly, a roadway was constructed in the 1960's on top of fill across the mouth of the fen, which mutes the hydrologic connection to Big Lagoon. This may affect salinity, water movement and wave action within Big Lagoon Bog and may have aided in the growth of woody vegetation.

The primary objective of our study was to investigate the impacts of woody vegetation encroachment on herbaceous species richness and cover within Big Lagoon Bog. Specifically, this study aimed

to quantify the relationship between woody vegetation encroachment and herbaceous species richness. In addition, this study aimed to update the botanical species lists for Big Lagoon Bog and map areas of highest herbaceous species diversity and special status plant species occurrences.

METHODS

Site Description

Big Lagoon Bog is a 1.3 ha peatland located in Big Lagoon County Park, Humboldt County (41.161580°, -124.129399°). It is situated within a shallow depression on the southwest corner of Big Lagoon (Fig. 1). Big Lagoon is a brackish embayment at the mouth of Maple Creek and separated from the Pacific Ocean by a sand barrier that is typically breached in winter months by storm water, affecting the water level and salinity of the lagoon. Water levels within Big Lagoon directly affect the water levels within Big Lagoon Bog. However, a small perennial stream flows through Big Lagoon

Bog from southeast to north that originates in forests dominated by *Sequoia sempervirens* (D. Don) Endl. (coast redwood, Cupressaceae) in the upper watershed and *Picea sitchensis* (Bong.) Carrière (Sitka spruce, Pinaceae) in the lower watershed. The upper watershed is managed for timber production, while the lower portions of the watershed – including Big Lagoon Bog – are primarily located within public lands including Big Lagoon County Park and Humboldt Lagoons State Park. The area surrounding the fen was logged in the late 1800's and converted to farmed and grazed lands which continued through the 1930's. Currently the area directly surrounding the fen is dominated by an 85-year-old even-age *P. sitchensis* forest that dates back to a cessation in grazing. Woody shrub and tree encroachment is occurring from all sides of Big Lagoon Bog and radially from numerous points within the fen (D Imper, United States Fish and Wildlife Service, G Leppig, California Department of Fish and Wildlife, D York, California Department of Transportation, personal communication).

Data Collection

We established 25 permanent transects by evenly dividing the length of Big Lagoon Bog from north to south and developing transects running west to east across the fen to ensure that the entire fen was adequately sampled (Fig. 2). Transects were 12m apart. We marked end points for each transect with PVC pipe stakes set in forest soils at the edge of the fen at both ends of each transect. Coordinates for end points were recorded with a Trimble 6T GPS unit (Trimble, Inc., Sunnyvale, CA). We collected plant community composition and species dominance data using 1x1 m quadrats placed 4 m apart from a random start point along transects.

We collected data from July 11 to August 16, 2018, during the time when herbaceous species are most easily identified. We recorded all vascular plant species and their percent cover for each species within every plot. Individual species and their corresponding percent cover were recorded within either herb stratum or woody stratum. The herb stratum included litter, thatch, large woody debris (LWD), bare ground, water and sphagnum percentages in addition to cover by non-woody plant species for a total of 100%. The woody vegetation stratum included all woody vegetation within and above the quadrat including trees and shrubs of any size. Cover included percent cover by each woody species for a total less than or equal to 100%. To avoid inflated cover estimates that would influence the analysis on the effect of total woody vegetation cover on herbaceous species cover and species richness, we excluded areas of direct overlap to prevent double counting. In addition, the extent of fen soils in relation to the start and end point of each transect was documented to assess the influence that distance from the edge of fen soil has on woody vegetation

encroachment. Also recorded were incidental occurrences of special status plant species and invasive species.

Analyses

We created Generalized Linear Models to assess the relationship between woody vegetation encroachment and herbaceous species richness. Histograms and correlation tests of the variables were conducted prior to development of a suitable model to determine multicollinearity. We used ANOVA to assess which variables would be appropriate for use in the model. Models were created using percent woody vegetation cover, percent litter cover, distance from the edge of the fen, woody vegetation height, and woody vegetation species richness as predictors of herbaceous species richness. Models were created assuming non-normally distributed data and the Poisson function for herbaceous species richness. Hypothesis tests (including goodness of fit, residuals, dispersion, and significance of terms) were conducted on the models in addition to Akaike Information Criteria (AIC). Several different model iterations were developed prior to the creation of the model that best fit the data using the above tests. The predicted values from the model and those from the data set were graphed to display the predictive power of the model and to compare observed values with values predicted by the created model. Following model creation, predicted outputs were visually displayed to show the relationship between the predictor variables and herbaceous species richness. Modeling and data analyses were conducted using R version 3.5.2 (R Foundation for Statistical Computing, Vienna, Austria). Visual displays of the model outputs were created using the *visreg* package in R version 3.5.2.

RESULTS

A total of 79 species were observed within Big Lagoon Bog over the course of this study. Of these, 75 species (95%) were present within the study plots. Nine additional species previously unrecorded for Big Lagoon Bog were observed. These consisted primarily of common species that occur within the vicinity of the fen, including the invasive *Hedera helix* L. (English ivy, Araliaceae). Of the total species observed, 22 were woody species and 57 were herbaceous species, of which eight are special status plant species and 11 are non-native species. We did not include species occurring outside of the extent of organic fen soil, or portions of the fen north of the access road (Fig. 2).

Within the 1x1 m study plots, average species richness was 8.4 species across the entire fen (range = 1 to 21). Plots were composed of an average of 3.8 (SE: 0.09) woody species and 4.6 (SE: 0.23) herbaceous species. The most diverse plot (21 species) was located in the center of the fen where the stream,

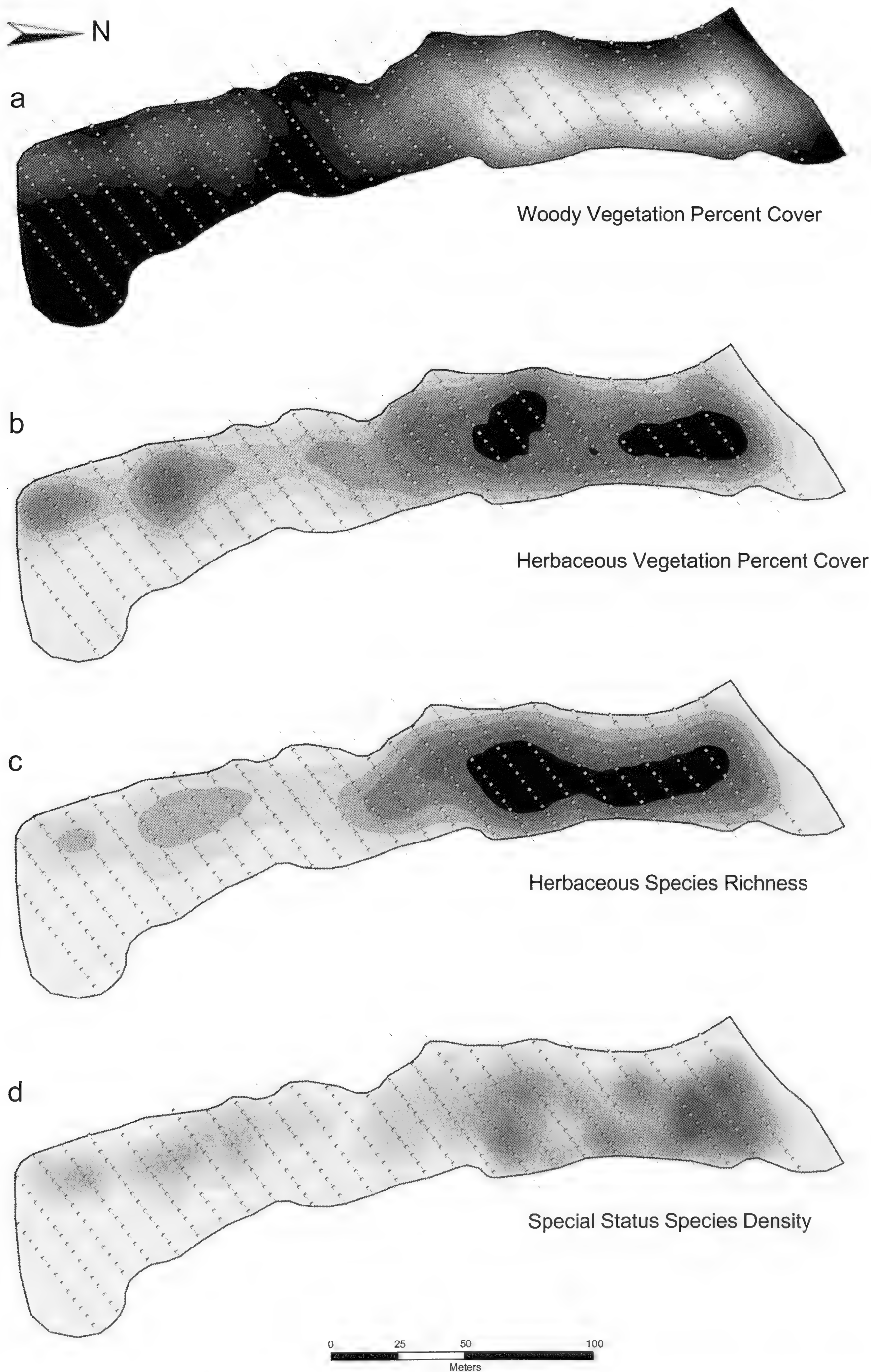


FIG. 2. Heat maps of Big Lagoon Bog showing the percent cover of woody and herbaceous plants (Panels a and b), herbaceous species richness (Panel c), and the density of special status species (Panel d). Dotted lines indicate transect and plot locations. Highest cover and density are depicted by the darkest color, and lowest cover and density are depicted by the lightest color.

TABLE 1: THE 12 MOST ABUNDANT TAXA FOUND IN THE STUDY OF BIG LAGOON BOG. Abundance is the average percent cover of the species within study plots (N = 338 plots). Frequency of occurrence is the percentage of study plots in which a species was observed.

Scientific Name	Common name	Percent cover of fen (standard error)	Frequency of occurrence (% of plots present)
<i>Picea sitchensis</i>	Sitka spruce	19% (± 1.69)	52%
<i>Morella californica</i>	California wax-myrtle	10.9% (± 1.05)	45%
<i>Ledum glandulosum</i>	western labrador tea	10.5% (± 0.80)	60%
<i>Struthiopteris spicant</i>	deer fern	9.1% (± 0.85)	57%
<i>Lysichiton americanus</i>	skunk-cabbage	6.9% (± 0.73)	42%
<i>Calamagrostis nutkaensis</i>	Pacific reed grass	5.1% (± 0.60)	35%
<i>Sphagnum</i> sp.	sphagnum	4.9% (± 0.72)	25%
<i>Spiraea douglasii</i>	Douglas spirea	4.8% (± 0.57)	41%
<i>Salix hookeriana</i>	coastal willow	3.8% (± 0.81)	12%
<i>Malus fusca</i>	Oregon crab apple	3.8% (± 0.81)	11%
<i>Rubus ursinus</i>	California blackberry	3.4% (± 0.23)	62%
<i>Gaultheria shallon</i>	salal	2.6% (± 0.38)	29%

which is channelized throughout the woody species-dominated portions of the fen, fans out into shallow, surface-flowing water (Fig. 2, Panel c). The least diverse locations within Big Lagoon Bog were within the southeastern portion of the fen under dense *P. sitchensis* cover, which in several instances was the only species present within the plot (Fig. 2, Panel c).

Eight of the 11 special status plant species previously recorded in Big Lagoon Bog were observed during the study, while the three remaining special status plant species (*C. leptalea*, *J. nevadensis* var. *inventus*, and *V. uliginosum*) were not observed and their continued persistence at this site is unknown. Special status plant species density was closely related to herbaceous species richness and cover, with the highest density of special status plant species occurring in the north-central portion of the fen, as well as the a small area in the southwestern portion of the fen, corresponding to a small remnant opening (Fig. 2, Panel d).

Dominant species included primarily woody species; *P. sitchensis* exhibited the highest level of total average cover within the fen (19%) and was present in 52% of the plots. *Rubus ursinus* Cham. & Schltdl. (California blackberry, Rosaceae) was the most frequently occurring species observed in 62% of the plots, with a total average cover of 3.4% within the fen (Table 1). Other woody dominants included *Morella californica* (Cham. & Schltdl.) Wilbur (California wax myrtle, Myricaceae; 10.9% average cover), *Ledum glandulosum* (Piper) Harmaja (Western Labrador tea, Ericaceae; 10.5% average cover), and *Spiraea douglasii* Hook. (Douglas spiraea, Rosaceae; 4.8% average cover; Table 1). Dominant herbaceous species included *Struthiopteris spicant* (L.) F.W.Weiss (deer fern, Blechnaceae; 9.1% average cover), *Lysichiton americanus* Hulten & H.St.John (yellow skunk-cabbage, Araceae; 6.9% average cover), and *Calamagrostis nutkaensis* (J.Presl) Steud. (Pacific reed grass, Poaceae; 5.1% average cover; Table 1). Of the 11 non-native species observed, five are invasive. *Rubus armeniacus* Focke

(Himalayan blackberry, Rosaceae), *Hypocheris radicata* L. (Hairy cat's-ear, Asteraceae), and *Cortaderia jubata* Stapf (jubata grass, Poaceae) were most prevalent of the invasive species observed. However, the non-native *Eleocharis pachycarpa* E.Desv. (broad fruit spikerush, Cyperaceae) was the most abundant non-native species, exhibiting 1.4% total average cover, followed by *Danthonia decumbens* (L.) DC. (mountain heathgrass, Poaceae), 2.2% total average cover.

Woody vegetation height within Big Lagoon Bog was primarily between 0 and 10 m, with a few plots containing woody vegetation over 10 m representing mature *P. sitchensis* on the eastern and western edges of the fen. Average woody vegetation height was 2.78 m, which included open areas with very little woody vegetation cover. Woody vegetation cover ranged between 0 and 100% cover, with very few plots containing 0% cover. Average woody vegetation cover across the entire fen was 69.3%, but woody vegetation was most dense along the edges of the fen and within the entire southeastern portion of the fen (Fig. 2, Panel a). Herbaceous species cover ranged between 0 and 100% cover, with few plots recording 100% cover by herbaceous species. Average herbaceous species cover across the entire fen was 41%, (SE: 1.75) and was highest in the north central portion of the fen where woody vegetation cover was lowest (Fig. 2, Panel b).

The Generalized Linear Model was a good predictor of the relationship between woody vegetation variables and herbaceous species richness within Big Lagoon Bog, and met the hypothesis test, dispersion (0.98), and goodness of fit criteria ($P > 0.22$) (Table 2). AIC indicated that the model using these predictor variables was better than models using fewer variables. The model indicated that increased woody vegetation cover, woody vegetation height, and increased litter cover are negative predictors of herbaceous species richness. The model also indicated that distance from the edge of the fen

TABLE 2: GENERALIZED LINEAR MODEL FOR PREDICTING HERBACEOUS SPECIES RICHNESS IN BIG LAGOON BOG. The full model included the following predictors: Woody Vegetation Cover, Litter Cover, Distance from the edge of the Fen, Woody Vegetation Height, and Woody Vegetation Species Richness. All variables were significant predictors of herbaceous richness, and diagnostic tests confirm the suitability of the full model.

Model:				
Herb Richness ~ Woody Cover + Litter + Distance + Woody Height + Woody Richness, family = Poisson				AIC
Full				1310.4
Reduced				1441.5
Full model dispersion: 0.98				
Goodness of fit: $P > 0.22$				
Model parameter	Estimate	SE	z	P-value
Intercept	2.2003	0.0869	25.310	< 0.0001
Woody vegetation cover	−0.0106	0.0014	−7.843	< 0.0001
Litter cover	−0.0124	0.0015	−8.434	< 0.0001
Distance from edge of fen	0.0107	0.0036	2.975	0.0029
Woody vegetation height	−0.0446	0.0129	−3.460	0.0005
Woody vegetation richness	0.0542	0.017612	3.079	0.0021

and woody vegetation species richness are positive predictors of herbaceous species richness.

Our model indicated that increasing woody vegetation cover is a good predictor of decreased herbaceous species richness (e.g., 65% woody vegetation cover should result in a 50% reduction in herbaceous species richness; Table 2, Fig. 3, Panel a), increasing litter cover is a predictor of decreased herbaceous species richness (58% litter cover should result in a 50% reduction of herbaceous species richness; Fig. 3, Panel b), and increasing height of woody vegetation is a predictor of decreased herbaceous species richness; (woody height of 16 m should result in a 50% reduction of herbaceous species richness; Fig. 3, Panel c). Both distance from the edge of fen and woody species richness were predictors of increased herbaceous species richness (35 m distance from the edge of the fen should result in a 50% increase in the number of herbaceous species). Similarly, the presence of seven woody vegetation species should result in a 50% increase of herbaceous species richness (Fig. 3, Panel e).

DISCUSSION

This study provides strong evidence that woody vegetation encroachment has been a primary driver of herbaceous species abundance and distribution loss in Big Lagoon Bog. In addition, if encroachment continues, decreases in herbaceous species richness and abundance will continue to occur across additional parts of the fen. These declines are likely to be occurring at numerous other similar coastal fen habitats that are known to be decreasing in size due to encroachment. Our study can be used to estimate the thresholds that exist for maintaining herbaceous species diversity in fens and wetlands currently in the process of woody vegetation encroachment, and our methodologies can be applied to other fens. In addition, our study suggests that the removal of woody vegetation may be a viable restoration technique within fens and other wetland types

currently being impacted by woody vegetation encroachment in the absence of natural disturbance.

Woody vegetation cover and woody vegetation height were found to have a strong negative relationship with herbaceous species richness and cover (Figs. 2 and 3, Panels a, b, and c). Effects from woody vegetation height are likely a result of decreasing light availability and increasing competition with herbaceous species in the understory (Coomes and Grubb 2000). In addition, woody vegetation height is a measure of the age of woody vegetation and a proxy measure of the age of encroachment. Litter cover is a direct result of woody vegetation encroachment, with increasing woody vegetation encroachment associated with an increase in litter deposition. The decrease in herbaceous species richness associated with increasing litter cover is likely a result of changes in soil conditions (Diemer et al. 2001), primarily a loss of saturated bare soils. Many of the herbaceous species present within the fen require bare organic soils for germination, and increasing litter deposition will raise the soil level above the water table, creating dry conditions that are not suitable for germination or persistence of wetland-dependent species (Diemer et al. 2001). Drier soil conditions resulting from increased woody vegetation can also create favorable conditions for additional non-native species introductions or expansion of existing non-native species cover. In addition, litter is likely to suppress diminutive herbaceous species such as *Sphagnum* sp., *D. rotundifolia*, and *L. inundata*.

Herbaceous species richness was found to be highest in the center of the fen where woody vegetation cover was low to non-existent, and the water table is at or near the soil surface (Figure 3, Panel c). Woody vegetation is less dense and is much younger in the center of the fen, allowing for greater herbaceous species richness. Increasing species richness of woody vegetation reflects the earliest stages of woody vegetation encroachment. Many woody vegetation seedlings may be present in plots with

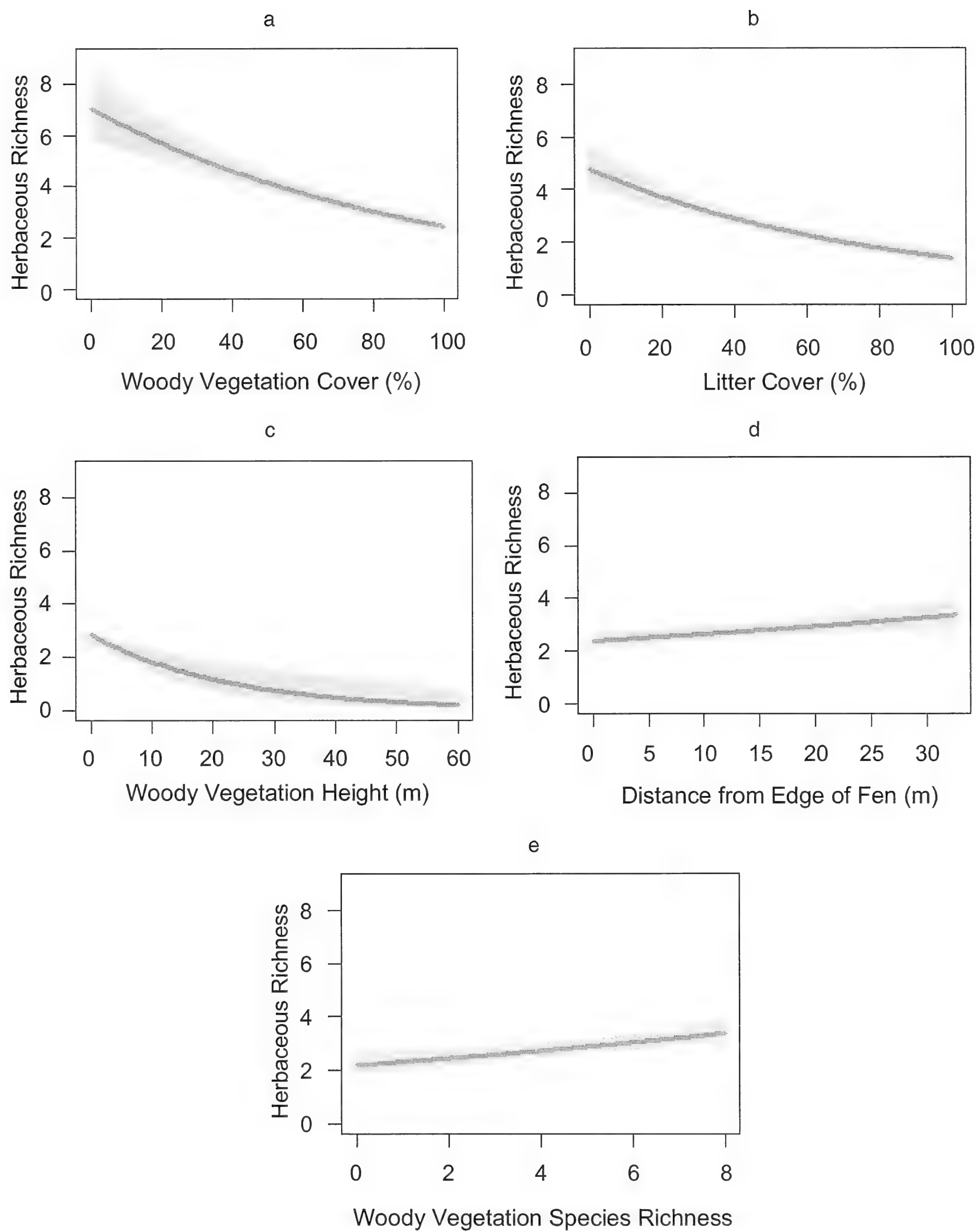


FIG. 3. Response of herbaceous species richness to five predictor variables, (a) woody vegetation cover, (b) litter cover, (c) woody vegetation height, (d) distance from the edge of fen, and (e) woody vegetation.

low woody vegetation cover and high herbaceous species richness, signaling the beginning of woody vegetation encroachment. Over time, as the woody species mature, fewer species will be present within a square meter as some become shaded and others become dominant. Plots with the highest number of woody vegetation species therefore indicate pre-

encroachment or early successional conditions within Big Lagoon Bog, with high herbaceous species diversity. Plots within these locations frequently had 15 or more herbaceous species present, and close to 100% cover by herbaceous species. Dominant herbaceous species within these portions of the fen varied. However, *C. nutkaensis* and *Deschampsia*

cespitosa ssp. *cespitosa* (L.) P.Beauv (tufted hairgrass, Poaceae) were common dominants.

Areas of the fen with the highest overall species diversity were also found to harbor the highest special status plant species densities. Special status plant species were found only in locations with little to no woody vegetation cover, and were completely absent from locations with woody vegetation canopy closure (Figure 3, Panel d). The absence of special status plant species from areas with woody vegetation canopy closure indicates that special status plant species are more sensitive to woody vegetation encroachment than some of the generalist herbaceous species, and likely will be the first species to be extirpated from the fen following moderate closure of the woody vegetation canopy. Special status plant species are often restricted to very specific habitat conditions (Mouillot et al. 2013) restricting them to small, select portions of the fen. When these areas become dominated by woody species, conditions change so that the area is no longer suitable for the support of the special status plant species previously found at that location. An example of this is *C. leptalea*, which was last recorded within the fen in 2012 (G Leppig, California Department of Fish and Wildlife, personal communication) in an area now dominated by an encroaching woody vegetation canopy. Similarly, *L. inundata* was historically observed in several locations throughout the fen but is now restricted to a few individuals within a remnant opening surrounded by a closed woody canopy. Our study indicates that continued woody vegetation encroachment will likely result in the decline or extirpation of many special status plant species from Big Lagoon Bog, in addition to the majority of the herbaceous species that are currently found within the fen.

The results from this study have implications for the future of fens and other herbaceous dominated wetlands in California and other temperate climates. The persistence of herbaceous species diversity and special status plant species within protected fens and wetlands is in jeopardy as a result of changes in disturbance regimes, which has allowed for the establishment and dominance of woody species. Without the return of some form of natural disturbance regime to these systems to maintain open, early successional habitat, it is likely that a complete shift to woody species domination will occur at the expense of herbaceous species diversity and dominance (Bowles et al. 1996; Matthias 2001; Güsewell and Le Nédec 2004; Middleton et al. 2006; Warren 2007). The loss of herbaceous species diversity has been qualitatively observed in coastal fens within the Pacific Northwest as a result of woody vegetation encroachment (Baker 1972; Christy 1979; Bencie and Kalt 2007), but no recent observations have been made in these fens to determine their condition at the present time. Herbaceous species richness has been seen to decrease in grasslands and savannas worldwide as a

result of woody vegetation encroachment (Ratajczak et al. 2012). Because special status plant species occurrences are frequently the result of random introductions (Leppig 2002; Sikes et al. 2013), it will be difficult to restore species diversity within fens and wetlands following the loss of herbaceous species due to woody vegetation dominance.

Woody vegetation was removed at Big Lagoon Bog following the completion of this study, but it will take at least several years to assess the effectiveness of this treatment. It may be that removal of woody vegetation can reset succession within partially encroached wetland systems, but it is unclear how effective it will be in restoring herbaceous diversity within fens and wetlands that have been impacted by a greater degree of woody vegetation encroachment. The loss of herbaceous species richness may be permanent if restoration is done following complete canopy closure and extirpation of herbaceous species from the site, depending on the longevity and dynamics of their seedbanks. The results from this study suggest that the removal of woody vegetation is a potential restoration method in fen and wetland habitat undergoing woody vegetation encroachment. The study also suggests that litter should be removed at the same time, through either burning or manual means, as the presence of litter will likely prevent the germination of herbaceous species. Removal of woody species and litter prior to the extirpation of herbaceous species may be sufficient in resetting succession within encroached fens and wetlands, thereby maintaining and restoring herbaceous species richness and dominance.

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NOMENCLATURAL NOTES ON TWO WESTERN *TRICHOSTEMA*

R. KEVAN SCHOONOVER MCCLELLAND AND ALAN S. WEAKLEY
Department of Biology, University of North Carolina, 120 South Road,
Chapel Hill, NC 27599
schoonor@live.unc.edu

ABSTRACT

Two species of *Trichostema* L. (Ajugoideae, Lamiaceae) from western states need nomenclatural clarification. *Trichostema simulatum* Jeps. occurs throughout northern California and southern Oregon. It was published by Willis Linn Jepson in his 1925 flora of California citing the type collection as “Klamathon, Copeland 3534, Type”. This is a conflation of the collector’s name and the specimen number of the exsiccata West American Plants, in which the type specimen was distributed by C. F. Baker in 1903. Furthermore, an herbarium name, “*Trichostema laetum* Greene,” appears on most *T. simulatum* type material. This designation was never published and is a *nomen nudum*. *Trichostema austromontanum* F.H.Lewis occurs throughout the mountain ranges of southern California and Baja California. Originally published with two subspecies by Harlan Lewis in 1945, the three taxa have since been determined to be invalidly published because Lewis did not provide a species description, only subspecies descriptions. Herein, we provide a clarification on the type specimens of *T. simulatum* Jeps. as well as a valid publication of the species name *T. austromontanum*.

Key Words: California, Lamiaceae, nomenclature, *Trichostema austromontanum*, “*Trichostema laetum*”, *Trichostema simulatum*, type specimens.

Trichostema is a genus of 19 species in the Lamiaceae, subfamily Ajugoideae, endemic to North America. California is one of the centers of diversity for this genus, with 11 of the 19 species occurring in the state (Baldwin et al. 2012). One section of the genus, *Orthopodium*, includes nine species, three of which are Californian endemics (Baldwin et al. 2012, Lewis 1945). Within this section, the nomenclature of two species of *Trichostema* require of clarification or validation: *T. simulatum* Jeps. and *T. austromontanum* F.H.Lewis. The publication of *T. simulatum* was in Jepson’s Flora (1925), wherein the author cited his type specimen as “Klamathon, Copeland 3534, type.” Other specimens of this species have been labeled as co- and isotypes since the original publication. All of these specimens were distributed by C. F. Baker and have labels with the heading “Plants of the Pacific Coast,” the designation “*Trichostema laetum* Greene n. sp.,” the exsiccata number 3534 from Baker’s Fall 1903 volume of exsiccata West American Plants, and have the collector information as “Dr. E. B. Copeland” with no collection number (s.n.). The exsiccata number and collector number were conflated in the designation of the type by Jepson. The designation “*T. laetum* Greene” was never published and is a *nomen nudum*. The publication of *T. austromontanum* and its two subspecies, subsp. *austromontanum* and subsp. *compactum*, was in a monograph of *Trichostema* by Lewis (1945) in which he failed to provide a description for his new species. Rather, he described only the two subspecies. Thus, the three names are invalid based on Art. 35.1 and Art. 38.1 of the Shenzhen Code (Turland et al. 2018).

Trichostema simulatum

Willis L. Jepson originally named *T. simulatum* in the first edition of *A Manual of the Flowering Plants of California* (1925). Therein, Jepson provides a description of the species and a designation of a type specimen, citing the collection “Copeland 3534,” thus validly publishing his new species name. However, there is an issue with the citation of the type specimen in both Jepson (1925) and Lewis (1945). They cite the collector and collection number as “Copeland 3534,” assuming that 3534 was Copeland’s collection number. This is incorrect. The pamphlet published by C.F. Baker shows that this number is the specimen number of his exsiccata West American Plants (Baker 1903). The collector and collection number should therefore be cited as “Copeland s.n.”

There has also been confusion regarding a designation, “*Trichostema laetum*,” present on the type specimens of *T. simulatum* that were distributed in the exsiccata by Baker (1903). This designation is a *nomen nudum*, but not because it is from an exsiccata. Original publication or distribution in an exsiccata does not disqualify a designation from becoming a valid name; however, a description of the species must be published with the specimen (pre-January 1, 1953) or separately (post-January 1, 1953; Turland et al. 2018). “*T. laetum*,” does not have an accompanying description with the specimens in the exsiccata, nor was a species description published at a later date. While other plants originally given designations in West American Plants (e.g., Baker 1904) were later validly published by Greene (1904), no known description of “*T. laetum*” was ever made (W. K. Cawley, Univ. of Notre Dame, personal communication). Thus, “*T. laetum*” is a *nomen nudum*.

A survey of the type specimens of *T. simulatum* Jeps. showed that specimens labeled as “*T. laetum*” are what formed the basis of Jepson’s new species. Furthermore, a search on JSTOR Global Plants showed that four herbaria have identified specimens of *T. simulatum* as types of “*T. laetum*.” As this designation is a *nomen nudum*, it cannot have type specimens. Between the collection citation error and the confusion surrounding Greene’s designation, we wish to clarify the origin and appropriate treatment of the type specimens of *T. simulatum*.

Trichostema austromontanum

Trichostema austromontanum and its subspecies have been recognized since their publication in 1945. The species is a tetraploid, thus setting it apart from the diploids in section *Orthopodium*. *Trichostema austromontanum* has been shown to be a “good” species both genetically and morphologically (Lewis 1945; Huang 2008). *Trichostema austromontanum* subsp. *compactum* was given threatened species status (Wallace and Vizgirdas 1998; revoked Carlsbad Fish and Wildlife Office 2018), and is still a conservation priority in southern California. For these reasons, we feel it prudent to validate this species and its two subspecies.

TAXONOMIC TREATMENT

Trichostema simulatum Jeps., Man. Fl. Pl. Calif., 862, 1925. *Trichostema laetum* Greene nom. nud. C.F.Baker, W. Amer. Pl. 2:18. 1903. —Type: USA, CA, Siskiyou Co., Klamathon, in bed of dry run, 2 July 1903, E. B. Copeland s.n., distributed in W. Amer. Pl. 2, C. F. Baker, 1903, specimen 3534. (holotype: JEPS; isotypes: G, GH, K, MO, NDG, NY, RM, RSA, US).

There are at least 11 type specimens of *T. simulatum*: one each at Greene-Nieuwland Herbarium at Notre Dame (NDG43542), Rancho Santa Ana Botanic Garden (RSA0004017), Rocky Mountain Herbarium at the University of Wyoming (RM0004890), New York Botanical Garden (NY00444545), Jepson Herbarium at UC-Berkeley (JEPS2898), Royal Botanic Gardens at Kew (K000975288), Harvard (GH; 00002257), Conservatory and Botanical Garden of the city of Geneva (G00402120), Missouri Botanical Garden (MO; Accession number 205555), and two at the Smithsonian Institution (Barcodes US00810827 and US00119393).

The designated holotype of *T. simulatum* resides at UC/JEPS. This specimen lacks the original exsiccata label, which would have included the designation “*T. laetum* E.L.Greene n. sp.” and would have been labeled as “Plants of the Pacific Coast, Spermatophytes and Ferns, Distributed by C.F. Baker.” This specimen instead has a label in Jepson’s hand (D. W. Taylor, UC/JEPS, personal communication), containing the locality and collector information from

the exsiccata label, the name “*Trichostema simulatum* Jepson n. sp.,” and “type” written in the upper right corner of the label. Using JSTOR Global Plants, a search for “*Trichostema simulatum*” returned seven type specimens: one identified as the holotype (the specimen from JEPS), five identified as isotypes (the specimens from G, GH, MO, and US), and one identified as a syntype (the specimen from K). A similar search for “*Trichostema laetum*” returned four specimens identified as types: one identified as the holotype (NDG), one identified as a “type?” (RM), and two identified as isotypes (NY and RSA).

The specimens themselves have various labels affixed to them that, at times, do not reflect their identification on JSTOR Global Plants. The specimens at GH, NY, MO, RSA, and one at US (US00810827) were labeled by Lewis in 1941 as isotypes of *T. simulatum*. The specimen from GH was also labeled as an isotype of that species by Philip Cantino in 1980. The specimen from NY was labeled as an isotype of “*T. laetum*” by an unknown person at an unspecified date. The specimen from RSA has no label calling it a type of “*T. laetum*” despite being identified on JSTOR as such. The specimen from K was labeled a co-type of *T. simulatum* by Lewis in 1947. The specimen at G was labeled as an isotype of *T. simulatum* by an unknown person after the year 2000 (the year on the label is “20__”). The specimens NDG43542, RM0004890, and US00119393 have no labels affixed to the specimens regarding type status for either *T. simulatum* or “*T. laetum*.”

As a holotype was designated for *Trichostema simulatum* (JEPS2898; Lewis 1945), all other specimens of *T. simulatum* collected by E. B. Copeland, s.n., on July 2, 1903, from Klamathon, CA, and distributed in C. F. Baker’s exsiccata West American Plants as specimen 3534 are hereby considered isotypes of that species and should not be considered types of any kind of “*T. laetum*.”

Trichostema austromontanum F.H.Lewis ex K.S.McClell. & Weakley. —Type: USA, CA, Riverside Co., Lake Hemet, 30 July 1941, H. Lewis 1479. (holotype: UCLA; isotype: UCLA).

Annual herb to 50 cm.; stems densely to loosely branching, hirtellous with short downwardly curved or appressed hairs, pilose with long straight hairs 0.5–1.5 mm long, occasional short capitate glands; leaves elliptic, 2–5 cm long, 0.3–1 cm wide, usually greater than four times as long as wide, shorter to much longer than the proceeding internode, apex acute, margin entire, base subcuneate, tapering to an indefinite petiole up to 5 mm long, pubescence similar to the stems; cymes axillary, congested, 1-many flowered, averaging 2 cm long, peduncles 1–5 mm; calyces with similar pubescence to the leaves, five lobed, lobes equal, deltoid to lanceolate, apex acute, broadest at the base, 1.6–2.5 mm long, lengthening in maturity to 2–3.8 mm, tube 0.6–1.2 mm long, lengthening in maturity to 1–1.8 mm;

corolla tube 1.5–3 mm long, more or less equal to the calyx lobes, five lobed, anterior lobe 1.8–3 mm long, deflexed; stamens arching, 3–5.5 mm long; nutlets 1.2–2 mm long, 0.8–1.2 mm wide, reticulate with sharp ridges, hirtellous to essentially glabrous; $2n = 28$.

This species is a tetraploid (the only one known in the genus) and is similar in form and habit to *T. oblongum* (a diploid), which genetic evidence suggests might be its parent (Huang et al. 2008). The two differ slightly in leaf dimensions (*T. oblongum* typically has wider, oblong leaves rather than elliptical leaves) and flowering time (*T. austromontanum* flowers June–October whereas *T. oblongum* flowers June–September). The most easily recognized difference between the two is the absence in *T. austromontanum* of the constriction at the base of the calyx lobes that is diagnostic of *T. oblongum*.

Trichostema austromontanum F.H.Lewis ex K.S.McClell & Weakley subsp. ***austromontanum***. — Type: USA, CA, Riverside Co., Lake Hemet, 30 July 1941, *H. Lewis 1479*. (holotype: UCLA; isotype: UCLA).

Annual herb typically 10–50 cm; stems loosely branching, internodes generally longer than 2 cm.; leaves 2–5 cm. long, as long as or shorter than the proceeding internode; corolla tube 1.5–3 mm. long, anterior lobe 1.8–3 mm. long; nutlets hirtellous.

Trichostema austromontanum subsp. *austromontanum* occurs in scattered populations from the central Sierra Nevada south through the Transverse Ranges and into the Peninsular Ranges of Baja California at elevations of 3500–7500 ft. It has a longer flowering time (June–October) than subsp. *compactum* (July–August). This subspecies also tends to be more robust than its parent species *T. oblongum*, which would be predicted based on its polyploid nature.

Trichostema austromontanum subsp. ***compactum*** F.H.Lewis. — Type: USA, CA, Riverside Co., Hidden Lake, 7 August 1928, *Martha Hilend s.n.*. (holotype: UC).

Annual herb typically smaller than 10 cm; stems densely branching, giving a compact appearance, internodes generally less than 2 cm long; leaves slightly smaller than *T. austromontanum* subsp. *austromontanum*, and due to the compact nature of the plant, much longer than the proceeding internode; flowers slightly smaller than *T. austromontanum* subsp. *austromontanum*; nutlets essentially glabrous.

This subspecies is known only from a single population near Hidden Lake in Riverside County, CA. This population is isolated at an elevation of approximately 8000 ft. It has been shown to maintain its morphology when grown in a common garden with the typical subspecies, suggesting that there is more than just an environmental basis to the

differing phenotypes (Lewis 1945). Genetic studies are pending.

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THE FLORA OF BIRD HAVEN RANCH, GLENN COUNTY, CALIFORNIA

KONSHAU DUMAN AND ELLEN DEAN

Center for Plant Diversity, Department of Plant Sciences Mail Stop 7, University of California, Davis, One Shields Avenue, Davis, CA 95616
kduman@ucdavis.edu

LYNETTE B. WILLIAMS AND ANDREW ENGILIS JR.

Museum of Wildlife and Fish Biology, Department of Wildlife, Fish, and Conservation Biology, University of California Davis, One Shields Avenue, Davis, CA 95616

ABSTRACT

This flora documents the vascular plant diversity of Bird Haven Ranch, a privately owned property with restored wetlands, rice fields, and riparian habitat, located in the Northern Sacramento Valley in eastern Glenn County, CA. Bird Haven Ranch is managed as waterfowl habitat. With increasing acreage of the Sacramento Valley being converted to restored wetland habitat, it is important to understand what plant taxa occur in these areas. We collected specimens documenting 57 families, 159 genera, and 222 vascular plant taxa, of which 58 percent were non-native. Thirty-six of the taxa collected represent new specimen records for Glenn County. Noteworthy collections from this project that add to our knowledge of the native flora of the floor of the north Sacramento Valley include *Chlorogalum pomeridianum* (DC.) Kunth var. *pomeridianum*, *Perideridia kelloggii* (A.Gray) Mathias, and *Stuckenia striata* (Ruiz & Pav.) Holub. In addition, two special-status plants, *Hibiscus lasiocarpus* Cav. var. *occidentalis* (Torr.) A. Gray, and *Azolla microphylla* Kaulf. were encountered during the survey.

Key Words: California, flora, Glenn County, waterfowl habitat, wetland restoration.

This study provides a preliminary flora for Bird Haven Ranch (Bird Haven), a 1020-hectare area of rice fields, restored wetlands, disturbed edge habitat, and riparian sloughs located in the northern part of the Sacramento Valley in southeastern Glenn County, CA. Bird Haven is located on the east side of the Sacramento River, on the north and south sides of County Road 67, and west of Butte Creek; central coordinates are 39.420132°N, –121.898130°W (Figs. 1 and 2). Bird Haven is privately owned and managed as a hunting club, with preference to supporting overwintering waterfowl, and is part of an expanding network of private lands restored to support waterfowl habitat in the Central Valley. Between the early 1980's and 2011, restored wetlands in the Central Valley grew from 153,000 hectares to 198,000 hectares (Duffy and Kahara 2011). The land that is now Bird Haven was originally used to raise cattle and sheep during the early 1900's (McComish and Lambert 1918). According to the current owner, grazing in the area of Bird Haven was carried out mostly on natural grasslands and woodlands with minimal habitat modification. These grazing lands were replaced with rice cultivation between 1967–1972, and rice has remained the primary crop since that time. Approximately 50% of the rice acreage was then restored to managed wetlands in the early 2000's. With the majority of restored lands in the Central Valley being devoted to wetland and riparian habitats like Bird Haven, it is important to understand what plants will colonize these newly created systems, as well as which native plants are likely to persist in these areas. This survey also helped provide

habitat information to support ongoing, long-term avian surveys carried out at Bird Haven by the University of California, Davis, Museum of Wildlife and Fish Biology.

Topography, Geology, and Climate

Bird Haven's topography is flat, with elevations ranging from 20 to 24 m above sea level. The nearest relief change is the foot of the Sutter Buttes, which is 13 km to the southeast. The only small elevation changes on the property are creek and slough edges, as well as human-made levees and road banks. The major drainages at Bird Haven are Butte Creek, Campbell Slough, and Howard Slough; there are also smaller unnamed sloughs and drainages that run through the property (Fig. 2).

Bird Haven Ranch lies on over 200 feet of unconsolidated Quaternary Alluvium comprising the Basin Deposits (USGS 2019). These deposits are composed of silt and clay carried from the surrounding mountains by the Sacramento River and its tributaries, which makes them excellent for agricultural production (California Department of Water Resources 2014). The soil of the property is primarily clay-rich vertisols with no visible horizons and a very homogeneous texture (UC Davis California Soil Resource Lab and NRCS 2019).

The area has a Mediterranean climate characteristic of the Sacramento Valley with hot dry summers and cool wet winters. There is extensive natural flooding at Bird Haven during most winters, as well

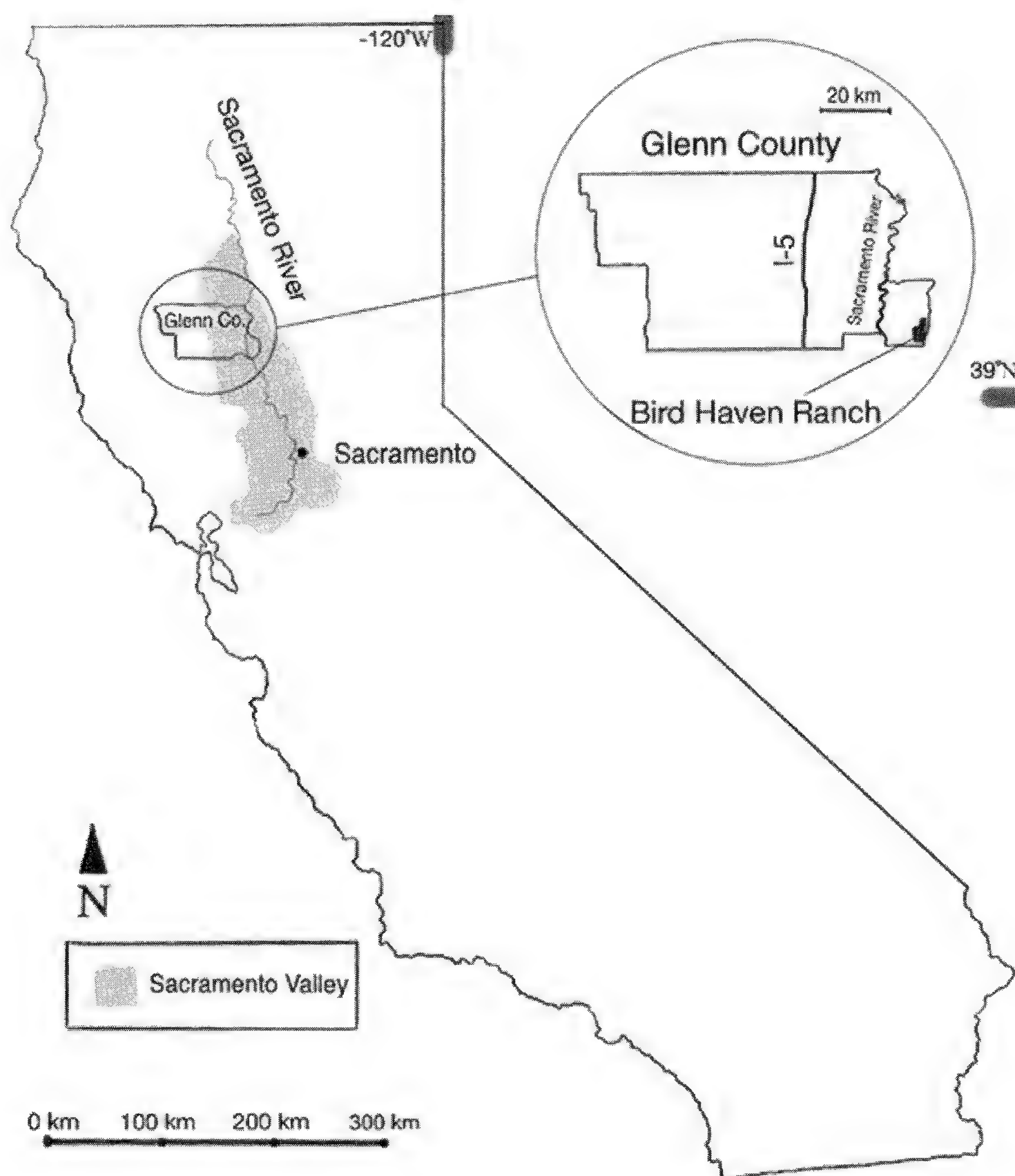


FIG. 1. Map of California showing the Sacramento Valley, Glenn County, and Bird Haven Ranch.

as managed flooding of wetland areas and rice fields to create habitat for wintering waterfowl.

Floristic History

Glenn County spans the Inner Coast Range in the west and the Sacramento Valley in the east. Historically, the flora of the eastern portion of the county has been poorly sampled. The eastern half has approximately half the number of specimen records as the western half, which contains national forest lands (CCH1 2020; CCH2 2020). Most lands in the eastern half are agricultural and privately owned with limited public access. The earliest plant collections from the Sacramento Valley portion of Glenn County were made in the late 19th century by botanists Joseph Burt Davy and Willis Lynn Jepson. These botanists mainly concentrated their efforts near Willows, now along Interstate 5, on the western side of the Sacramento River, near the present-day Sacramento National Wildlife Refuge (CCH1 2020). The area of the county that includes the Sacramento National Wildlife Refuge continued to be of interest to botanists in the 20th century, and a flora of the Refuge was completed in 1995 (Oswald and Silveira

1995). Other than this, most botanical surveys in the 20th century concentrated on the Inner Coast Range part of the county (Heckard and Hickman 1985; CCH1 2020). This is in contrast to the numerous collections made in the Sacramento Valley in Butte County by botanists associated with the herbarium at the California State University, Chico, some of which were made relatively close to Bird Haven (Oswald and Ahart 1994; CCH1 2020).

Prior to our study, there were no plant collections from the lands that comprise Bird Haven. The only collections from the immediate vicinity were made along Road 67 adjacent to the property: one of *Hibiscus lasiocarpus* Cav. var. *occidentalis* (Torr.) A.Gray (R. Hill 38549 [CAS-BOT-BC277735]) and the other of *Abutilon theophrasti* Medik. (L.P. Janeway 10107 [CHSC104772]). Post-2001 restoration projects at Bird Haven did not introduce any herbaceous species, and plantings were limited to *Salix gooddingii* C.R.Ball and *Populus nigra* L. *Salix gooddingii* has naturally regenerating stands in the riparian and restored wetland areas, but *P. nigra* has no apparent regeneration. Crops currently planted at Bird Haven include corn (*Zea mays* L.), sorghum (*Sorghum bicolor* (L.) Moench), rice (*Oryza sativa*

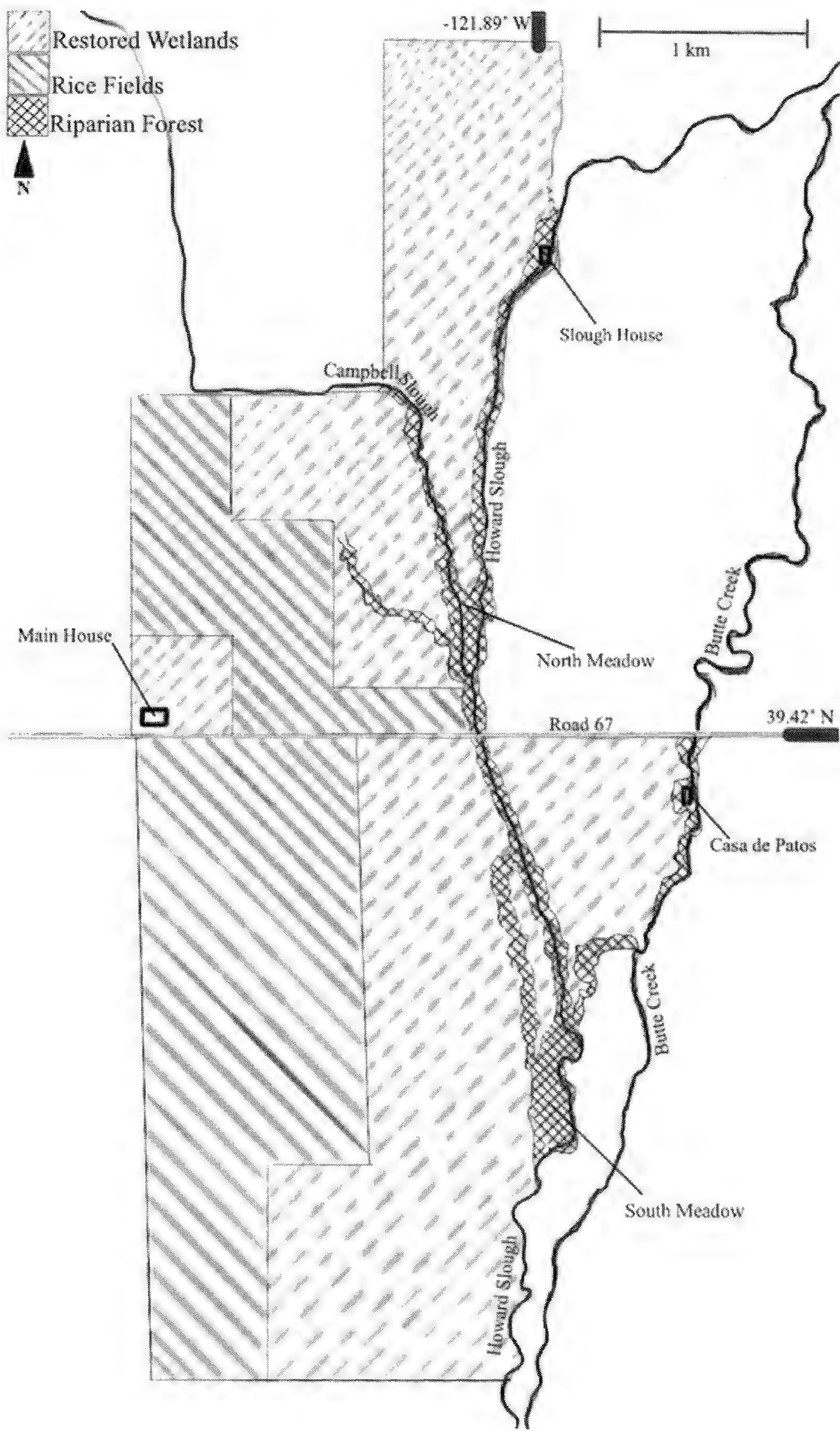


FIG. 2. Map of Bird Haven Ranch showing the primary habitat types and important locations on the property that are referenced in Noteworthy collections (Table 1) and on specimen labels.

L.), barley (*Hordeum vulgare* L.), peas (*Pisum sativum* L.), and beans (*Phaseolus vulgaris* L.); other row crops or ornamental plants may have been cultivated/planted in the past.

METHODS

Before commencement of the floristic survey, a list of special-status plants with potential to occur at Bird Haven was compiled by performing a database search of the California Native Plant Society’s

Electronic Inventory of Rare and Endangered Vascular Plants of California (CNPS 2020). Bird Haven was surveyed by motorized cart and on foot. Eight two-day-long collecting trips from 12 April 2019 to 29 September 2019 were conducted. Sixteen single day collecting trips were made in March–May 2020 to gather additional specimens. Field notes were recorded on the locations and occurrences of collected species, and relevant habitat details were noted. Decimal degree coordinates were documented for all specimens collected in the field using a

smartphone application. Specimens were initially determined using the Jepson Manual II (Baldwin et al. 2012), the Jepson eFlora (2020), and Flora of North America (FNA 1993+), and confirmed by comparison with existing specimens at the UC Davis Center for Plant Diversity herbarium where they were then deposited. All specimen label data can be accessed online at the Consortium of California Herbaria portal (CCH2 2020). The county specimen record status of our collections was determined through herbarium specimen searches using both the CCH2 portal and the Consortium of California Herbaria One portal (CCH1 2020).

RESULTS

Plant Collections

During our survey, 235 specimens were collected, representing 222 vascular plant taxa, 159 genera, and 57 families (Appendix 1). For the few taxa that were collected more than once, only the initial collection number is cited in Appendix 1. Of the taxa collected, 58 percent are non-native, which reflects the highly disturbed nature of the area. Thirty-six of the taxa collected are county specimen records (first herbarium specimen collected in the county, denoted by an asterisk in the list in Appendix 1), and two taxa collected were special-status species: *Hibiscus lasiocarpus* var. *occidentalis*, California Rare Plant Rank (CRPR) 1B.2, and *Azolla microphylla* Kaulf, CRPR 4.2 (CNPS 2020).

Vegetation and Habitats

The lands of Bird Haven Ranch have four main habitat types, with the vegetation of these habitats almost completely determined by the nature of human use, water management, and disturbance or lack thereof. These habitats are rice fields, restored wetlands, disturbed edge, and the riparian woodland and meadows that line Howard Slough, Campbell Slough, and Butte Creek (Fig. 2).

The rice fields are sown and flooded in late spring and early summer and remain flooded until late summer when they are drained before the rice is harvested in early fall. During this period, they support a variety of aquatic plants that grow among the rice stems, on the water's surface, and around the margins of the field. In some areas, stands of *Sagittaria*, *Cyperus difformis* L., and *Leptochloa fusca* (L.) Kunth subsp. *fascicularis* (Lam.) N.Snow grow denser than the rice itself or grow taller and shade it out. After the fields are drained and harvested, all these plants give way to tilled stubble which is again flooded in winter for straw degradation. Up until 2001 (when restoration projects began at Bird Haven), rice fields dominated nearly all the property, but they currently occupy only 36.9% of the total land area and are continuous across the western portion of Bird Haven. Only 31 plant taxa

(14% of those collected) were found in rice fields, of which 18 were native (58%).

Restored wetlands on the property consist primarily of managed seasonal marshes, which are divided into pond units with independent levee and water control structures to help regulate water depth and maintain independent water control. Management includes three hydrological systems. The first includes wetlands that are managed as summer-dry and winter-flooded (mimicking more natural hydrological cycles of the region). Second are marshes managed as moist-soil wetlands. Moist-soil management entails several summer pulses of water into wetland units to encourage the seed bank to develop dense stands of emergent annuals favored by waterfowl in winter months (Fredrickson 1991). These ponds have a moist meadow appearance, remaining green throughout the summer. Finally, each year, two to three ponds are flooded year-round as summer water to support broods of waterfowl. All these habitat management scenarios create a diversified wetland landscape on the property and are intended to lead to increased diversity of emergent plant species.

There is a rapid succession of annual vegetation that develops on the pond beds as soon as the water disappears, beginning with low annual grasses and forbs such as *Lythrum hyssopifolia* L., *Lythrum tribracteatum* Salzm. Ex Spreng., *Rorippa palustris* (L.) Besser, *Juncus bufonius* L., and *Cynodon dactylon* (L.) Pers., which form a lush carpet across the pond beds in spring. By early summer, these low-lying plants give way to and are shaded by tall and fast-growing plants like *Xanthium strumarium* L., *Abutilon theophrasti* Medik., *Ammi visnaga* (L.) Lam., and *Persicaria* species. These wetland areas also have large stands of *Schoenoplectus acutus* (Muhl. ex Bigelow) Á.Löve & D.Löve and *Typha latifolia* L., as well as *Salix gooddingii* C.R.Ball around the margins and on the raised islands. Besides flooding, these areas are spot treated with herbicide to control *Cynodon* and other unwanted weeds and mowed to create better habitat for waterfowl. There are also permanent ponds near the main buildings and water-filled ditches throughout. These host more of the submerged aquatic vegetation such as *Stuckenia striata* (Ruiz & Pav.) Holub, *Potamogeton crispus* L., and *Myriophyllum spicatum* L. Restored wetlands make up 50.6% of the total land area and hosted 133 taxa (60% of those collected) of which 54 (40%) were native.

Disturbed edge areas consist of dirt roads and access trails, mowed ditch banks, and field margins. They have primarily weedy herbaceous vegetation, which grows when the soil is moist in late winter and spring and sets seed and dries by late summer (July in 2019). These areas make up 6.7% of the land area and have 102 taxa (46% of those collected) of which 19 (19%) are native.

The riparian sloughs, woodland, and meadows are the only habitats on the property that were not

TABLE 1. Noteworthy collections made at Bird Haven Ranch. Taxa encountered during our survey with few to no collections from the northern Sacramento Valley floor. The Sacramento Valley region is defined here as in Baldwin et al. (2012).

Plant taxon	Significance
<i>Chlorogalum pomeridianum</i> subsp. <i>pomeridianum</i>	First specimen record from the Sacramento Valley floor, rather than adjacent to the foothills. Both previous specimen records from the Sacramento Valley region are within 5 km of the Sierra Nevada Foothills or Coast Range Foothills (e.g., <i>M.S. Taylor</i> 3053 [CHSC030089]; <i>B. Crampton</i> 9496 [AHUC37431]).
<i>Perideridia kelloggii</i>	Not recognized as occurring in the Sacramento Valley (ScV) or Great Valley (GV) region by Baldwin et al. (2012). This record represents one of the few specimen records of this species from the Sacramento Valley floor not adjacent to the foothills. Previously collected in Butte County and in the Sutter Buttes (CCH1 2020, CCH2 2020). Specimen much taller than the recognized height range cited by Baldwin et al. (2012), exceeding the upper limit by 43 cm.
<i>Stuckenia striata</i>	First specimen record from Glenn Co. and first from the Sacramento Valley. Very few collections in California with the nearest one located in Contra Costa County (<i>D. Slakey</i> 223 [DAV215263]) in the Sacramento-San Joaquin Delta 153 km away (CCH1 2020, CCH2 2020).

completely altered by agricultural disturbance nor created by recent restoration projects. The riparian habitats of Bird Haven comprise only 5.8% of the land area, but have 132 taxa (59% of those collected) of which 66 (50%) were native.

The sloughs are mostly in channels with steep banks, so that there is often little emergent vegetation between the water and the woodland understory. The woodland consists of an overstory of *Quercus lobata* Née, *Fraxinus latifolia* Benth., and *Acer negundo* L., with most of the canopy made up of *Q. lobata*. Given this composition, the riparian woodland at Bird Haven is most similar to the *Quercus lobata* Woodland Alliance of Sawyer et al. (2009). The understory of the woodland is variable, but often is composed of shrubby thickets of *Rubus armeniacus* Focke, *Vitis californica* Benth, and *Cephalanthus occidentalis* L., with an herbaceous layer of dense *Carex barbarae* Dewey or mixed annual grasses and forbs.

There are two small riparian meadow areas on the property that have depressions with seasonally waterlogged soil containing *Juncus xiphioides* E.Mey. *Sisyrinchium bellum* S.Watson, and *Eryngium castrense* Jepson, as well as open areas of grasses and forbs. The meadow vegetation changes radically through the season starting in spring with a low carpet of *Plagiobothrys* species, which by mid-June are overtaken by *Festuca perennis* (L.) Columbus & J.P.Sm. and other intermediate sized annuals. By late August, *Helianthus bolanderi* A.Gray and *Hemizonia congesta* DC. subsp. *luzulifolia* (DC.) Babco. & H.M.Hall form a layer about a meter tall across the entire meadow and cover the drying remains of the shorter-lived annuals. This cycle is renewed by annual mowing of the meadow areas and removal of the thatch. These riparian meadows probably represent a mixture of vegetation types, but they contain a number of species included in the *Juncus xiphioides* Provisional Herbaceous Alliance and the *Lasthenia glaberrima* Herbaceous Alliance of Sawyer et al. (2009).

DISCUSSION AND CONCLUSIONS

The lack of topography in the area of Bird Haven, combined with uniform soils, leads to a relatively homogeneous flora. As mentioned above, the only other published flora of an area located in the Sacramento Valley of Glenn County was completed at the Sacramento National Wildlife Refuge (SNWR) to the west of the Sacramento River (Oswald and Silveira 1995). The SNWR flora includes many of the same taxa found at Bird Haven with most of the overlap being ruderal plants of marshes and disturbed areas. There is much less overlap with riparian species at Bird Haven. Established in 1937, SNWR has a much longer history of preservation than Bird Haven, and much of the agricultural activity on the refuge ceased by the 1960’s. It also hosts alkali sink and vernal pool habitats that harbor many native and endemic plants. Perhaps for these reasons, the flora of SNWR has a lower proportion of non-native taxa (42% to Bird Haven’s 58%) and 13 special-status plants to Bird Haven’s two (CNPS 2020). However, Bird Haven has riparian woodland areas, which SNWR lacks, and is an excellent example of a similarly managed wetland habitat at an earlier stage in the restoration process.

The riparian woodland areas of the Sacramento Valley are highly threatened by continuing agricultural and urban development, and Bird Haven’s riparian corridor is one of only 180 patches of valley riparian woodland greater than 10 hectares in area (Hunter et al. 1999). This corridor has a disproportionate amount of the property’s plant diversity and native plant diversity, with over ten times the number of plant species and 12 times the number of native plant species per unit area than the property as a whole. The present study expands on our understanding of the flora of these woodlands with two species that have almost no collections in the Sacramento Valley: *Chlorogalum pomeridianum* and *Perideridia kelloggii* (Table 1). *Chlorogalum pomer-*

idianum was restricted to shaded areas of riparian understory where there was sparse herbaceous vegetation and no *Rubus armeniacus* thickets. Though it initially seemed restricted to one patch near Slough House in the north, further observation revealed additional scattered groups throughout the riparian woodland of the south side of the property as well. *Perideridia kelloggii* was only found in a part of the riparian woodland adjacent to a small meadow on the south side of the property, but was abundant in that area, forming large perennial stands with scattered plants in between them.

We collected thirty-six county specimen records during this study. Twenty-six are weedy non-natives and one is a native that causes dermatitis (*Toxicodendron diversilobum* (Torr. & A.Gray) Greene); these types of taxa are often ignored by collectors. Three others are aquatic natives that are often overlooked because of their diminutive size and ephemeral nature (*Callitriche heterophylla* Pursh, *Elatine rubella* Rydb., and *Limosella acaulis* Sessé & Moc.). The other six county specimen records are native species that are well-collected in other places in California, and that they had not yet been collected in Glenn County can only be explained by a lack of previous collection effort. They include both riparian and aquatic plants (*Cephalanthus occidentalis* Benth., *Cornus glabrata* Benth., *Juncus patens* E.Mey., and *Rorippa palustris* (L.) Besser subsp. *palustris*), as well as non-aquatic plants (*Brodiaea elegans* Hoover subsp. *elegans* and *Sisyrinchium bellum* S.Watson). Our flora helps to fill distributional gaps for these taxa in both Glenn County and the Sacramento Valley region.

ACKNOWLEDGMENTS

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APPENDIX 1. LIST OF TAXA COLLECTED AT BIRD HAVEN RANCH

Native taxa are in bold type; collector number in parentheses; taxa not previously collected in Glenn Co. marked with asterisk (*). Taxonomy and nativity follow the

Jepson eFlora (2020). Authors of plant names follow The Jepson Interchange (2020) with formatting of author names following IPNI (2020).

AGAVACEAE

Chlorogalum pomeridianum (DC.) Kunth var. *pomeridianum*

Uncommon. Open riparian woodland understory. *K. Duman* 85 (DAV230808).

ALISMATACEAE

Echinodorus berteroi (Spreng.) Fassett

Locally common. Irrigation ditch bottoms and rice field margins on soft mud with shallow water. *K. Duman* 108 (DAV230971).

Sagittaria longiloba Engelm. ex J.G.Sm.

Common. Rice field margins. *K. Duman* 149 (DAV232743).

Sagittaria montevidensis Cham. & Schltdl. subsp. *calycina* (Engelm.) Bogin

Uncommon. Rice field margins. *K. Duman* 212 (DAV232926).

AMARANTHACEAE

Amaranthus albus L.

Uncommon. Dirt roadways, field margins, and disturbed areas with annual vegetation. *K. Duman* 204 (DAV232588).

ANACARDIACEAE

**Toxicodendron diversilobum* (Torr. & A.Gray) Greene

Very common. Riparian woodland understory. *K. Duman* 11 (DAV230689).

APIACEAE

Ammi visnaga (L.) Lam.

Common. Restored seasonal wetland plots, on raised islands and margins in dense stands with *Mentha pulegium* L. *K. Duman* 162 (DAV233389).

Anthriscus caucalis M.Bieb.

Common. Dry disturbed areas with taller vegetation and open woodland. *K. Duman* 21 (DAV230507).

Conium maculatum L.

Locally common. Disturbed open areas. *K. Duman* 217 (DAV232370).

Eryngium castrense Jeps.

Uncommon. Vernal moist depressions in meadow openings in riparian woodland, S side of property. *K. Duman* 116 (DAV230815).

Perideridia kelloggii (A.Gray) Mathias

Locally common. Shaded riparian woodland understory adjacent to S meadow. *K. Duman* 206 (DAV232587), 130 (DAV232603), 226 (DAV233097).

Torilis arvensis (Huds.) Link

Uncommon. Open riparian areas. *K. Duman* 300 (DAV235108).

Torilis nodosa (L.) Gaertn.

Uncommon, but found throughout. Disturbed areas. *K. Duman* 99 (DAV230813).

APOCYNACEAE

Asclepias fascicularis Decne.

Locally common. Meadow openings and sparse riparian woodland understory in N and S ends of the property. *K. Duman* 155 (DAV232747).

ARACEAE

Lemna minuta Kunth

Common. Floating aquatic or stranded on exposed mudflats in sloughs, ditches and rice fields, often in association with *Azolla* species. *K. Duman* 211 (DAV232362).

ASTERACEAE

Achillea millefolium L.

Uncommon. Only found on a small stretch of the road that runs east from the Main House. *K. Duman* 45 (DAV230732).

Ambrosia psilostachya DC.

Common throughout. Riparian woodland openings and edges and restored wetland margins. *K. Duman* 294 (DAV235144).

Anthemis cotula L.

Common. Open disturbed areas and the S meadow where it is dominant in summer before being shaded out by *Helianthus bolanderi*. *K. Duman* 111 (DAV230822).

Artemisia douglasiana Besser

Uncommon. Riparian woodland understory and edges, elevated areas that dry out in summer. *K. Duman* 224 (DAV2333323).*Baccharis pilularis* DC. subsp. *consanguinea* (DC.) C.B.Wolf

Uncommon; perhaps intentionally planted. A few isolated bushes in open herbaceous vegetation in the SE part of the property. *K. Duman* 66 (DAV230639).

Bidens frondosa L.

Locally abundant. Flat bottom areas of open seasonal restored wetlands; often forming continuous patches late in the season. *K. Duman* 146 (DAV232725).

**Bidens tripartita* L.

Uncommon. Shaded ditch banks and levees at riparian woodland edge. *K. Duman* 222 (DAV233103).

**Carduus pycnocephalus* L. subsp. *pycnocephalus*

Common. Disturbed areas of tall unmowed herbaceous vegetation by ditches and road banks. *K. Duman 48* (DAV230722).

Centaurea solstitialis L.

Rare. Disturbed areas with tall drying annual vegetation. *K. Duman 46* (DAV230729).

**Cichorium intybus* L.

Uncommon. Disturbed areas with dry annual vegetation. *K. Duman 120* (DAV230816).

Cirsium vulgare (Savi) Ten.

Fairly common. Dry margins of restored wetlands and disturbed edges of riparian woodland. *K. Duman 156* (DAV232746).

**Cotula australis* (Sieber ex Spreng.) Hook.f.

Rare. Forming a dense carpet on the exposed gravel driveway at Casa de Patos. *K. Duman 251* (DAV234598).

Cotula coronopifolia L.

Rare. Only seen on the gravel driveway at Casa de Patos; growing with *Cotula australis* L. *K. Duman 271* (DAV234599).

Eclipta prostrata (L.) L.

Uncommon. In thick mixed annual vegetation of willow riparian understory and along irrigation ditch NE of Main House. *K. Duman 221* (DAV233500).

Erigeron bonariensis L.

Common but sparse. Edges of roads, mowed levees, and other disturbed areas with short annual vegetation. *K. Duman 110* (DAV230572).

Erigeron canadensis L.

Occasional throughout. Disturbed margins of riparian woodland, edges of restored wetland, and mowed road banks. *K. Duman 255* (DAV234615).

Erigeron sumatrensis Retz.

Common and widespread. Restored wetland areas, on small raised islands under the shade of *Salix gooddingii*. *K. Duman 102* (DAV230277).

Euthamia occidentalis Nutt.

Occasional throughout. Sparse riparian woodland, ditch banks, and restored wetland margins. *K. Duman 223* (DAV233319).

Gnaphalium palustre Nutt.

Locally abundant. Margins of raised islands in restored wetland areas and around the edges of drying ponds; forming continuous patches at the high-water mark early in spring before being overgrown by taller annuals. *K. Duman 109* (DAV230817).

Grindelia camporum Greene

Rare. Isolated plants found at the margins of dry wetland ponds. *K. Duman 243* (DAV233327).

Helianthus annuus L.

Rare; a single plant found, possibly escaped from cultivation. Edge of a restored wetland in the N part of the property. Observed only.

Helianthus bolanderi A.Gray

Locally abundant. Riparian woodland openings, and the S meadow; forming dense continuous stands over lower annual vegetation. *K. Duman 202* (DAV232930).

Helminthotheca echioides (L.) Holub

Common and widespread. Dry elevated areas along ditches, road banks, and restored wetland margins. *K. Duman 127* (DAV232604).

Hemizonia congesta DC. subsp. *luzulifolia* (DC.) Babc. & H.MHall

Rare. Found only in the S meadow, growing with *Helianthus bolanderi*. *K. Duman 203* (DAV232931).

Lactuca saligna L.

Common but sparse. Dirt roadways and mowed areas, especially near Slough House. *K. Duman 199* (DAV232933).

Lactuca serriola L.

Common and widespread. Along roads and ditches. *K. Duman 147* (DAV232726).

Lasthenia glaberrima DC.

Rare. Vernal moist depression in the S meadow. *K. Duman 69* (DAV230634).

Leontodon saxatilis Lam.

Uncommon. Along road banks in gravelly compacted soil, mainly in the S part of the property near Casa de Patos. *K. Duman 37* (DAV230506).

Matricaria discoidea DC.

Common and widespread. In mowed vegetation, usually along roads and trails. *K. Duman 73* (DAV230638).

Senecio vulgaris L.

Common and widespread. Road banks, ditches, field edges, and levees. *K. Duman 35* (DAV230689).

Silybum marianum (L.) Gaertn.

Uncommon; often growing as single plants and isolated stands. Along dirt roads and ditches, and on islands and margins of restored wetland areas. *K. Duman 97* (DAV230894).

Sonchus asper (L.) Hill subsp. *asper*

Common and widespread. Along levees, ditches, road banks, and drying wetland margins. *K. Duman 126* (DAV232589).

**Sonchus oleraceus* L.

Same habitat as *Sonchus asper*. Common. *K. Duman 64* (DAV230741).

Symphotrichum subulatum (Michx.) G.L.Nesom var. *squamatum* (Spreng.) S.D.Sundb.

Locally common. Restored wetland areas, often on raised islands, and herbaceous understory of riparian woodland,

especially in the SE edge of the property. *K. Duman 103* (DAV233499).

**Taraxacum officinale* F.H.Wigg.

Uncommon. Mowed areas; only found near Casa de Patos. *K. Duman 265* (DAV234600).

Xanthium strumarium L.

Common and widespread. Restored wetlands, riparian zones, and disturbed edges, forming continuous dense stands alongside *Abutilon theophrasti* late in the summer. *K. Duman 131* (DAV232606).

AZOLLACEAE

Azolla filiculoides Lam.

Common. Floating in rice fields, ditches, and sloughs with low water flow; often forming a continuous layer on water surface. *K. Duman 248* (DAV233104).

Azolla microphylla Kaulf.

Locally common. Floating in riparian sloughs. *K. Duman 41* (DAV230724).

BETULACEAE

Alnus rhombifolia Nutt.

Rare. Several mature trees along the bank of Butte Creek along the SE edge of the property. *K. Duman 33* (DAV230502).

BORAGINACEAE

Plagiobothrys bracteatus (Howell) I.M.Johnst.

Locally common in early spring. Areas of low annual vegetation and nearly bare ground, as well as bare ground of drying flooded fields. *K. Duman 249* (DAV233083).

Plagiobothrys stipitatus var. *micranthus* (Piper) I.M.Johnst.

Locally common. Riparian openings and bare ground in low annual vegetation, mainly in the S meadow in early spring; forming a carpet-like layer with *Plagiobothrys bracteatus*. *K. Duman 278* (DAV234614).

BRASSICACEAE

Brassica nigra (L.) W.D.J.Koch

Common and widespread, but not in dense stands. Along ditches and road banks. *K. Duman 65* (DAV230738).

Capsella bursa-pastoris (L.) Medik.

Common and widespread. In low mowed annual vegetation. *K. Duman 63* (DAV230739).

**Cardamine hirsuta* L.

Common early in the spring. In low annual vegetation, like mowed areas and newly emerging weedy patches. *K. Duman 253* (DAV234596).

Lepidium latifolium L.

Locally common. Gravelly disturbed areas by roads and levees, mainly along the paved road to the west of Slough House. *K. Duman 107* (DAV230820).

Lepidium strictum (S.Watson) Rattan

Rare. Exposed gravel driveways, mainly near the workshop south of the Main House. *K. Duman 266* (DAV234606).

Planodes virginica (L.) Greene

Locally common and widespread. Beds of drying restored wetland ponds (rarely in other moist open areas); growing with *Lythrum hyssopifolia* and *Juncus bufonius*. *K. Duman 79* (DAV230718).

Raphanus sativus L.

Uncommon but widespread. Margins of roads and ditches. *K. Duman 61* (DAV230737).

**Rorippa palustris* (L.) Besser subsp. *palustris*

Common and widespread. In open, low, annual vegetation in drying seasonal restored wetlands as well as in the margins of wetland areas. *K. Duman 114* (DAV230575).

CARYOPHYLLACEAE

Cerastium glomeratum Thuill.

Uncommon. In S meadow; in low, early spring, annual vegetation. *K. Duman 258* (DAV234593).

Polycarpon tetraphyllum (L.) L. var. *tetraphyllum*

Occasional. Openings in riparian woodland, disturbed edges, mowed areas, and restored wetland pond beds; growing with low annuals. *K. Duman 141* (DAV232738).

Spergularia rubra (L.) J.Presl & C.Presl

Common. In dirt roads; forming carpet-like patches in late spring. *K. Duman 89* (DAV232914).

Stellaria media (L.) Vill.

Common. In moist annual vegetation, especially in shade of riparian woodland. *K. Duman 34* (DAV230693).

CHENOPODIACEAE

Chenopodium album L.

Locally abundant. Riparian woodland understory; often a dominant in areas of tall herbaceous vegetation under *Quercus lobata* and *Fraxinus latifolia* in the SE edge of the property. *K. Duman 213* (DAV232360).

**Dysphania anthelmintica* (L.) Mosyakin & Clemants

Rare. Raised islands in restored wetland ponds and shaded riparian understory. *K. Duman 254* (DAV234595), 294 (DAV235144).

Dysphania pumilio (R.Br.) Mosyakin & Clemants

Uncommon and local. Margins of dirt roads; only found just south of Road 67, east of Howard Slough. *K. Duman 228* (DAV233318).

CONVOLVULACEAE

Convolvulus arvensis L.

Common. Very disturbed areas, such as newly graded roads, plowed fields, newly mowed roadways, and herbicide-treated areas. *K. Duman 70* (DAV230640).

Cuscuta campestris Yunck.

Locally common. In dry restored pond beds and formerly flooded fields; parasitic vine growing on newly emerging annuals like *Polygonum aviculare* and *Lythrum hyssopifolia*. *K. Duman 154* (DAV232749).

CORNACEAE

**Cornus glabrata* Benth.

Locally common. Riparian woodland along sloughs (most common along Howard and Campbell Sloughs where they converge); growing with *Cephalanthus occidentalis*. *K. Duman 14* (DAV230511).

CRASSULACEAE

Crassula aquatica (L.) Schönl.

Common and widespread. On mud of rice fields. *K. Duman 60* (DAV230720).

CYPERACEAE

Carex barbarae Dewey

Common and widespread. Riparian woodland: forms dense cover (and tolerates mowing) in well-shaded areas with little *Rubus armeniacus*. *K. Duman 6* (DAV230687).

Carex densa (L.H.Bailey) L.H.Bailey

Common. Riparian woodland understory and meadow openings; forms small, scattered tufts in shaded areas in both the N and S sides of the property. *K. Duman 94* (DAV233080).

Carex praeegracilis W.Boott

Common and widespread. Open riparian woodland and riparian openings; develops sprawling, wavy tussocks that cover parts of the small N meadow. *K. Duman 38* (DAV230509).

Cyperus difformis L.

Common. Margins and center of rice fields; forming dense stands. *K. Duman 209* (DAV232929).

Cyperus eragrostis Lam.

Common. Restored wetland and rice field edges as well as moist areas along riparian sloughs. *K. Duman 86* (DAV232923).

**Cyperus flavicomus* Michx.

Uncommon. Rice fields, mostly at margins. *K. Duman 219* (DAV233101).

Eleocharis macrostachya Britton

Locally common. Exposed or shallowly submerged mud of restored seasonal wetlands. *K. Duman 50* (DAV230721), 276 (DAV234617).

Schoenoplectus acutus (Muhl. ex Bigelow) Á.Löve & D.Löve

Common and widespread. Restored wetlands and riparian slough margins; forming dense stands in managed wetlands that are mowed back or disked to prevent the stands from filling in the open water areas. *K. Duman 40* (DAV230500).

ELATINACEAE

Elatine ambigua Wight

Common. On the submerged or slightly exposed mud of rice fields; forms carpets with *Crassula aquatica*. *K. Duman 167* (DAV232751).

**Elatine rubella* Rydb.

Common. Rice fields: growing while the fields are still shallowly flooded in early spring and persisting in small tufts of *Juncus bufonius*. *K. Duman 277* (DAV234608).

EQUISETACEAE

Equisetum hyemale L. subsp. *affine* (Engelm.) Calder & RoyL.Taylor

Rare. Riparian; on west bank of Butte Creek east of Casa de Patos. *K. Duman 299* (DAV235119).

EUPHORBIACEAE

Croton setiger Hook.

Occasional and widespread. Disturbed edge habitats; growing in scattered, low patches late in the summer. *K. Duman 142* (DAV232742).

**Euphorbia peplus* L.

Rare. Disturbed areas; a few individuals near Casa de Patos. *K. Duman 298* (DAV235118).

Euphorbia maculata L.

Uncommon. Dry road banks and dried pond bottoms; grows where other weedy annuals are sparse. *K. Duman 210* (DAV232359).

Euphorbia serpillifolia Pers.

Uncommon. Exposed ground in riparian openings and restored wetland pond bottoms; largely in the S meadow in late summer. *K. Duman 119* (DAV230895).

FABACEAE

Lathyrus jepsonii var. *californicus* (S.Watson) Hoover

Rare. Riparian woodland; one patch above Butte Creek east of Casa de Patos. *K. Duman 296* (DAV235116), 291 (DAV235114).

Lotus corniculatus L.

Common. On road and ditch banks, levees, restored wetland edges, and riparian areas; forms thick stands with *Medicago* species. *K. Duman 62* (DAV230742).

Lupinus bicolor Lindl.

Rare. In mowed exposed roadsides. *K. Duman 283* (DAV234604), 275 (DAV234616).

Medicago arabica (L.) Huds.

Common. Riparian woodland understory and edge, roadsides, and areas of exposed weedy vegetation; often with *Medicago polymorpha*. Observed only.

Medicago polymorpha L.

Common and widespread. Weedy open areas, margins of riparian woodland understory, and restored wetland margins. *K. Duman 18* (DAV230684).

**Melilotus albus* Medik.

Common and widespread. Riparian woodlands and meadows, as well as islands and margins in restored wetlands; scattered in areas of weedy annual vegetation. *K. Duman 101* (DAV230574).

Melilotus indicus (L.) All.

Common. Disturbed edges; often with the more common *Melilotus albus*. *K. Duman 123* (DAV232600).

**Pisum sativum* L.

Rare; only one plant found in the south meadow and possibly escaped from cultivation. *K. Duman 259* (DAV234592).

Trifolium fragiferum L.

Locally common. Mowed roads around the north brood pond NE of the main house across the rice fields. *K. Duman 303* (DAV235454).

Trifolium hirtum All.

Locally common. Margins of roads, levees, ditches, and other elevated areas with exposed annual vegetation and annual mowing; mainly found near Casa de Patos. *K. Duman 71* (DAV230635).

Vicia americana Muhl. ex Willd. subsp. *americana*

Uncommon and local. Edges and openings in riparian woodland on the SE edge of the property. *K. Duman 280* (DAV234602).

Vicia benghalensis L.

Locally abundant in the northern part of the S meadow in vernal moist soil with low exposed annual vegetation. *K. Duman 289* (DAV235147).

Vicia sativa L.

Common and widespread. On ditch banks, levees, raised margins of fields, and openings in riparian woodland. *K. Duman 54* (DAV230723).

Vicia villosa Roth

Common. Open areas of annual grasses and forbs, especially with stands of *Phalaris aquatica*. *K. Duman 281* (DAV234603).

FAGACEAE

Quercus lobata Née

Common. Riparian woodland: dominant overstory tree along all the sloughs (no evidence this species was planted). *K. Duman 12* (DAV230726).

GENTIANACEAE

Centaurium tenuiflorum (Hoffmanns. & Link) Jansch

Uncommon. Raised islands in restored wetland areas with *Salix gooddingii* shade in the S restored wetlands. *K. Duman 133* (DAV232601).

GERANIACEAE

Erodium botrys (Cav.) Bertol.

Common and widespread. In areas of mowed annual vegetation and in drying restored pond beds. *K. Duman 78* (DAV230636).

Erodium moschatum (L.) Aiton

Common and widespread. In herbaceous riparian understory, open areas of dry seasonal wetland, road banks, levees, and other disturbed areas. *K. Duman 20* (DAV230686).

Geranium carolinianum L.

Common and widespread. Mowed banks and roadsides, drying pond beds, wetland margins, and riparian woodland understory and openings. *K. Duman 17* (DAV230685), 270 (DAV234619).

HALOGORACEAE

Myriophyllum spicatum L.

Uncommon and local. Floating aquatic only found in the pond by the Main House as well as the ditch to the south of it. *K. Duman 159* (DAV233388).

IRIDACEAE

Iris pseudacorus L.

Uncommon and local. Margins of managed wetlands, usually in shade of *Salix gooddingii*; a few robust stands in the S portion of the property. *K. Duman 25* (DAV230678).

**Sisyrinchium bellum* S.Watson

Locally common. Meadow openings in riparian woodland; often scattered in vernal moist areas, growing among grasses, sedges, rushes, and annual forbs. *K. Duman 129* (DAV232602).

JUNCACEAE

Juncus bufonius L.

Common. Rice fields, flooded crop fields, and seasonal wetland areas; forming a sparse carpet on clumps of drying mud exposed in the spring. *K. Duman 59* (DAV230743).

Juncus mexicanus Willd.

Uncommon. Vernal moist depressions in riparian woodland openings and along the edges of sloughs. *K. Duman 77* (DAV230641).

**Juncus patens* E.Mey.

Common and widespread. Margins of restored wetland areas, especially those that are flooded and kept moist during the summer. *K. Duman 19* (DAV230510), 245 (DAV233328).

Juncus xiphioides E.Mey.

Common. Vernaly moist depressions in meadow openings in riparian woodland and shaded margins of managed wetland ponds. Often forming large continuous stands. *K. Duman 93* (DAV233081).

LAMIACEAE

Lycopus americanus W.P.C.Bartram

Common and widespread. Moist, shaded ground around the margins of the ponds of restored wetlands, especially those that remain flooded in the summer. *K. Duman 139* (DAV232739).

Mentha pulegium L.

Common. Margins of restored wetland ponds and the islands within them; often forming a dense continuous patch along the high-water line. *K. Duman 163* (DAV233466).

Stachys ajugoides Benth.

Uncommon. Meadows in both the N and S parts of the property and occasional in restored wetlands scattered in sparse clumps of a few individuals. *K. Duman 118* (DAV230812), 292 (DAV235143).

LYTHRACEAE

Ammannia coccinea Rottb.

Common in rice fields and uncommon in summer-flooded wetlands. *K. Duman 207* (DAV232961).

Lythrum hyssopifolia L.

Common and widespread. Riparian areas, disturbed edge, and restored wetland ponds; most abundant on open mud of drying wetland ponds. *K. Duman 83* (DAV232924).

**Lythrum salicaria* L.

Rare. Single plant found on the south bank of Road 67. *K. Duman 144* (DAV232728).

Lythrum tribracteatum Salzm. ex Spreng.

Occasional. Same habitats the more common *Lythrum hyssopifolia*. *K. Duman 164* (DAV233465).

MALVACEAE

Abutilon theophrasti Medik.

Common. Restored wetland and disturbed edge areas; often forming large stands alongside *Xanthium strumarium*. *K. Duman 137* (DAV232741).

Hibiscus lasiocarpus Cav. var. *occidentalis* (Torr.) A.Gray

Common and widespread. Restored wetland areas and riparian sloughs; forms robust stands of one to many individuals, often with willows or *Schoenoplectus acutus* in open marshy areas. *K. Duman 205* (DAV232737).

**Malva parviflora* L.

Common and widespread. In open areas of herbaceous vegetation, especially where it is regularly mowed or disturbed. *K. Duman 56* (DAV230736).

Malvella leprosa (Ortega) Krapov.

Common. Growing in areas of dry soil and dried annual grasses and forbs in summer. *K. Duman 201* (DAV232922).

MARSILEACEAE

Marsilea vestita Hook. & Grev. subsp. *vestita*

Rare. Only found on the dry bed of a restored wetland pond that sits inside of the westward bend in Campbell Slough in the N section of the property; collected in the fall. *K. Duman 237* (DAV233099).

MOLLUGINACEAE

Mollugo verticillata L.

Locally common but widespread. In areas of dry soil and sparse annual vegetation. *K. Duman 158* (DAV233387).

MONTIACEAE

Calandrinia menziesii (Hook.) Torr. & A.Gray

Rare. Single plant found on a mowed exposed levee with low annual vegetation in the SE corner of the property. *K. Duman 257* (DAV234594).

MORACEAE

Ficus carica L.

Occasional but widespread. Riparian woodland; often growing near *Morus alba*. *K. Duman 9* (DAV230682).

**Morus alba* L.

Occasional but widespread. Riparian woodland, mainly on the north side of the property, especially around Slough House; often growing near *Ficus carica*. *K. Duman 10* (DAV230690).

MYRSINACEAE

Lysimachia arvensis (L.) U.Manns & Anderb.

Uncommon but widespread. Disturbed ground with little to no vegetative cover. *K. Duman 125* (DAV232591).

OLEACEAE

Fraxinus latifolia Benth.

Common and widespread. Riparian woodland: with *Quercus lobata*, forms the main canopy and sub-canopy structure of native riparian woodland on the property. *K. Duman 13* (DAV230681).

ONAGRACEAE

Epilobium brachycarpum C.Presl

Common and widespread. Disturbed areas with weedy annual vegetation, often on dry gravelly road banks. *K. Duman 235* (DAV233321).

Epilobium densiflorum (Lindl.) Hoch & P.H.Raven

Locally common. Restricted to vernal moist area in low annual vegetation on the upper bank of Butte Creek. *K. Duman 250* (DAV233464).

Ludwigia peploides (Kunth) P.H.Raven

Common and widespread. Ditches, sloughs, and wetland areas with standing water in summer; often forming continuous mats in open areas of sloughs and ditches. *K. Duman 138* (DAV232745).

PHRYMACEAE

Erythranthe guttata (DC.) G.L.Nesom

Rare. Restored wetland; on berm between ponds on bare soil with *Juncus bufonius* and *Planodes virginica*. *K. Duman 58* (DAV230735).

PHYTOLACCACEAE

Phytolacca americana L. var. *americana*

Uncommon. Elevated ground in riparian woodland in the N and S portions of property. *K. Duman 214* (DAV232361).

PLANTAGINACEAE

Bacopa rotundifolia (Michx.) Wettst.

Common and widespread. In rice fields, especially in open water near the margins. *K. Duman 151* (DAV232748).

**Callitriche heterophylla* Pursh

Uncommon. In moist rice fields in early spring before they are plowed, growing in small patches with *Juncus bufonius* on raised clumps of soil. *K. Duman 263* (DAV234607).

Kickxia spuria (L.) Dumort.

Common and widespread the property in the weedy margins of roads. Often forming sprawling patches with high ground cover for a brief period in spring. *K. Duman 31* (DAV230504).

Plantago lanceolata L.

Common. Vernal moist depressions in open areas of riparian woodland and riparian meadow, as well as open weedy areas. *K. Duman 42* (DAV230730).

Plantago major L.

Common. Sympatric with *Plantago lanceolata* but slightly less common. *K. Duman 132* (DAV232605).

Veronica anagallis-aquatica L.

Occasional and local. Marshy bottom of the ditch in the NW corner of the property; growing in and around stands of *Typha domingensis* in waterlogged soil. *K. Duman 106* (DAV230573).

Veronica peregrina L. subsp. *xalapensis* (Kunth) Pennell

Common and widespread. Open areas of drying restored wetlands, disturbed areas with low annual vegetation, and open areas in riparian woodland; initially a dominant herb in drying ponds. *K. Duman 51* (DAV230734).

POACEAE

Agrostis avenacea J.F.Gmel.

Uncommon but widespread. Open weedy patches of restored wetland areas. *K. Duman 80* (DAV230632).

Avena barbata Pott ex Link

Common and widespread. Road banks, ditch margins, and areas of tall unmowed weedy vegetation. *K. Duman 43* (DAV230725).

Avena fatua L.

Common and widespread. Disturbed weedy areas with taller vegetation; much less common than *Avena barbata* but occurring in the same habitats. *K. Duman 96* (DAV233469).

Bromus diandrus Roth

Locally common but widespread. Areas of dry weedy annual vegetation with minimal to no mowing, such as in riparian woodland understory and open disturbed edges. *K. Duman 24* (DAV230505).

Bromus hordeaceus L.

Common and widespread. Open areas of annual vegetation (often mowed) and in riparian openings. *K. Duman 44* (DAV230733).

Crypsis schoenoides (L.) Lam.

Common and widespread. Dry pond beds in restored wetlands; often carpeting areas of cracked dry mud, especially after summer flooding. *K. Duman 145* (DAV232610).

Cynodon dactylon (L.) Pers.

Common and widespread. Riparian woodland understory, moist riparian openings, restored wetland ponds, and disturbed edge areas with low annual cover; often carpeting drying pond beds and vernal moist depressions. *K. Duman 74* (DAV230644), 104 (DAV233468).

Digitaria ischaemum (Schreb.) Muhl.

Uncommon. Margins of restored wetlands that are flooded in summer. *K. Duman 140* (DAV232740).

Digitaria sanguinalis (L.) Scop.

Locally common. Edges of rice fields and other crop fields within restored wetland areas, especially in the N part of the property. *K. Duman 218* (DAV233102).

Echinochloa colona (L.) Link

Found in tilled and irrigated areas of annual crop fields dispersed within restored wetland areas. Locally common between the crops and around the margins in dispersed patches. *K. Duman 239* (DAV233322).

Echinochloa crus-galli (L.) P.Beauv.

Very common and widespread. Present in all habitats on the property, especially where there is summer moisture, but

most abundant in drying restored wetland ponds; this species is managed heavily on the ranch, as the seeds are a preferred and important food item for wintering waterfowl. *K. Duman 152* (DAV232744).

**Echinochloa oryzoides* (Ard.) Fritsch

Rare. Found only by a culvert at the S end of "Woody Hole" in standing water of an irrigation ditch. *K. Duman 227* (DAV233498).

Elymus glaucus Buckley subsp. *glaucus*

Common and widespread. Dry elevated areas in restored wetlands, disturbed edge habitats, and riparian woodland. *K. Duman 98* (DAV230571).

**Elymus hispidus* (Opiz) Melderis

Common and widespread. Open disturbed areas, riparian woodland edges, and elevated margins of restored wetlands; often forms dense continuous stands. *K. Duman 26* (DAV230512).

Eragrostis hypnoides (Lam.) Britton, Sterns & Poggenb.

Rare. Found in bed of N brood pond NE of the Main House. Two carpet-like patches. *K. Duman 303* (DAV235455).

Eriochloa contracta Hitchc.

Locally common. Elevated areas of restored wetland ponds and margins of irrigated annual crop fields in the N section of the property. *K. Duman 242* (DAV233326).

**Glyceria declinata* Bréb.

Common. Rice fields: grows in tufts around *Juncus bufonius* on elevated clumps of soil after the winter flooding recedes. *K. Duman 274* (DAV234604).

Hordeum brachyantherum Nevski subsp. *brachyantherum*

Locally common. Vernal moist areas in openings of riparian woodland. *K. Duman 91* (DAV233082).

Hordeum marinum Huds. subsp. *gussoneanum* (Parl.) Thell.

Common and widespread. Dry exposed areas with sparse low annual vegetation such as dirt roads and mowed levees. *K. Duman 286* (DAV234612).

Hordeum murinum L.

Common and widespread. Disturbed edges, riparian woodland understory, and restored wetland margins. *K. Duman 23* (DAV230688).

Leptochloa fusca (L.) Kunth subsp. *fascicularis* (Lam.) N.Snow

Common. Exposed areas with standing water in summer, such as rice fields and restored wetlands. *K. Duman 208* (DAV232928).

Festuca perennis (L.) Columbus & J.P.Sm.

Common and widespread. In areas with open herbaceous vegetation, such as riparian woodland where it often fills in much of the understory and openings by mid-summer. *K. Duman 82* (DAV230809).

Oryza sativa L.

A few escaped individuals found in moist soil of an irrigation ditch at the W edge of the property just N of Road 67. *K. Duman 232* (DAV233105).

Paspalum dilatatum Poir.

Common and widespread. Road banks, rice field margins, slough banks, and other areas with summer moisture and disturbance. *K. Duman 220* (DAV233100).

Paspalum distichum L.

Common. Margins of sloughs and restored wetland ponds late in the summer. *K. Duman 241* (DAV233325).

Phalaris aquatica L.

Very common and widespread. Raised open ground around the margins of restored wetlands and alongside roads and ditches (including mowed areas); one of the most abundant herbaceous plants on the property, forming dense perennial stands in areas that are not flooded. *K. Duman 32* (DAV230697), 92 (DAV233384).

Phalaris brachystachys Link

Uncommon. Tilled margins of annual crop fields. *K. Duman 281* (DAV234613).

Phalaris paradoxa L.

Uncommon. Disturbed open riparian woodland edges and tilled field margins. *K. Duman 124* (DAV232590).

Poa annua L.

Common. Almost entirely restricted to dirt roads and trails early in spring. *K. Duman 287* (DAV234622).

**Poa infirma* Kunth

Uncommon. On the surface of compacted dirt roads in the S section of the property; occurring alongside *Poa annua*. *K. Duman 252* (DAV234597).

Polypogon monspeliensis (L.) Desf.

Locally common. In areas of low (or mowed) annual vegetation, both along roads and around Casa de Patos. *K. Duman 72* (DAV230633).

Setaria pumila (Poir.) Roem. & Schult. subsp. *pumila*

Uncommon. In moist ditches and along the banks of sloughs on the N side of the property. *K. Duman 200* (DAV232932).

Sorghum halepense (L.) Pers.

Common and widespread. Along ditches, roadsides, restored wetland ponds, and riparian woodland edges. *K. Duman 22* (DAV230691).

Festuca myuros L.

Occasional but widespread. In areas of mixed grasses and weedy vegetation, especially along dirt road banks. *K. Duman 36* (DAV230677).

POLYGONACEAE

Persicaria amphibia (L.) Delarbre

Occasional but widespread. On the banks of sloughs in riparian woodland and margins of restored wetland ponds and rice fields. *K. Duman 268* (DAV234601).

Persicaria maculosa Gray

Common. Restored wetlands, ditches, rice field margins, and other moist habitats, very common on drying pond beds. *K. Duman* 288 (DAV234621), 290 (DAV235146).

**Persicaria pensylvanica* (L.) M.Gómez

Common and widespread. Managed wetland areas and rice field margins; this species, which can regrow from previous year’s stems and act as a perennial, along with *P. maculosa*, it can quickly outgrow other emergent plants and is actively managed to maintain open marsh habitat. *K. Duman* 49 (DAV230719).

Polygonum aviculare L.

Common. Areas of low annual vegetation, especially mowed areas, tilled field margins, and dirt roads. *K. Duman* 88 (DAV230806).

Rumex conglomeratus Murray

Common. In areas with tall weedy annual vegetation, especially around restored wetland areas and riparian woodland edges. *K. Duman* 29 (DAV230676).

Rumex crispus L.

Common and widespread. Riparian woodland, restored wetlands, and disturbed edge areas; found in unmowed annual vegetation and moist soils. *K. Duman* 47 (DAV230731).

**Rumex pulcher* L.

Uncommon. In areas of open, annual vegetation in riparian woodland understory. *K. Duman* 216 (DAV232369).

PONTEDERIACEAE

Heteranthera limosa (Sw.) Willd.

Common and widespread. Rice fields: floating and emergent in the center and margins of rice fields early in the season before the rice becomes dense and shades the surface of the water. *K. Duman* 160 (DAV232750).

PORTULACACEAE

**Portulaca oleracea* L.

Uncommon. Exposed gravel roads and driveways. *K. Duman* 148 (DAV232727).

POTAMOGETONACEAE

Potamogeton crispus L.

Uncommon. Only found in the pond by the Main House and nearby irrigation channels. Dense stands in these areas. *K. Duman* 230 (DAV233106).

**Stuckenia striata* (Ruiz & Pav.) Holub

Uncommon. In slow-moving water of the ditch S of the Main House; occurs mixed with *Potamogeton crispus*. *K. Duman* 231 (DAV233320).

RANUNCULACEAE

Ranunculus muricatus L.

Uncommon. In S meadow near riparian woodland; in low herbaceous cover, especially where mowed. *K. Duman* 117 (DAV230819).

ROSACEAE

Rosa californica Cham. & Schltdl.

Common and widespread. Riparian woodland understory; often growing with *Rubus armeniacus*. *K. Duman* 95 (DAV233470).

**Rosa canina* L.

Occasional in the S section of the property. Wooded margins of restored wetlands and edge of riparian woodland; ranging from a mounded shrub to a climber reaching 3–5 m in height. *K. Duman* 67 (DAV230637).

Rubus armeniacus Focke

Very common and widespread. Forming dense thickets in riparian woodland understory: this plant is actively controlled by the ranch to prevent overgrown thickets. *K. Duman* 87 (DAV230818).

**Rubus pensilvanicus* Poir.

Rare. Riparian understory; growing alongside *Rubus armeniacus* near Slough House. *K. Duman* 279 (DAV234620).

RUBIACEAE

**Cephalanthus occidentalis* L.

Common and widespread. Riparian woodland: forming dense thickets on the banks of sloughs, generally shaded by taller riparian trees. *K. Duman* 134 (DAV232608).

Galium aparine L.

Common and widespread. Riparian woodland, disturbed edges, and restored wetland margins. *K. Duman* 27 (DAV230501).

SALICACEAE

Populus fremontii S. Watson subsp. *fremontii*

Occasional but widespread. Riparian woodland and restored wetland margins; only isolated trees observed. This species is managed in restored wetlands on the ranch to maintain open marsh habitat*K. Duman* 52 (DAV230728).

Populus nigra L.

Occasional. Planted in rows alongside restored wetland ponds as a wind break. *K. Duman* 157 (DAV233467).

Salix babylonica L.

Rare. Riparian woodland; a few naturalized trees near Road 67. *K. Duman* 229 (DAV233107).

Salix exigua Nutt. var. *hindsiana* (Benth.) Dorn

Common and widespread. Restored wetland margins and openings in riparian woodland. *K. Duman* 75 (DAV230643).

Salix gooddingii C.R.Ball

Very common and widespread. Restored wetlands (planted and managed) and riparian woodland (occurring naturally). *K. Duman 28* (DAV230692).

Salix laevigata Bebb

Uncommon. Isolated trees in restored wetland area margins and riparian woodland. Always mixed with *Salix gooddingii*. *K. Duman 76* (DAV230642).

Salix lasiolepis Benth.

Common. Exposed ditches and sloughs in riparian woodland. *K. Duman 30* (DAV230503).

SAPINDACEAE

Acer negundo L.

Common and widespread. Riparian woodland. Along with *Fraxinus latifolia*, forms the primary sub-canopy of *Quercus*-dominated riparian woodland, present in both shrub and tree form. *K. Duman 7* (DAV230683).

Acer saccharinum L.

Rare. Exposed area along Butte Creek. *K. Duman 240* (DAV233324).

SCROPHULARIACEAE

**Limosella acaulis* Sessé & Moc.

Uncommon. Moist, unplowed rice fields in early spring; growing in small patches of *Juncus bufonius* on raised clumps of soil. *K. Duman 262* (DAV234609).

Verbascum blattaria L.

Occasional throughout. Disturbed, exposed edges and riparian woodland. *K. Duman 57* (DAV230740).

Verbascum thapsus L.

Rare. Disturbed areas; two plants near Casa de Patos. *K. Duman 297* (DAV235117).

SOLANACEAE

Physalis acutifolia (Miers) Sandwith

Rare. In low annual vegetation above the bank of Butte Creek. *K. Duman 166* (DAV233463).

Physalis lanceifolia Nees

Rare. S meadow. *K. Duman 161* (DAV233462).

Solanum nigrum L.

Occasional throughout. Shaded margins of restored wetlands and riparian woodland. *K. Duman 267* (DAV234610).

THEMIDACEAE

**Brodiaea elegans* Hoover subsp. *elegans*

Uncommon. Meadow openings of riparian woodland. *K. Duman 128* (DAV232607).

Triteleia laxa Benth.

Rare. S meadow in early spring. *K. Duman 68* (DAV230645).

TYPHACEAE

Typha domingensis Pers.

Locally common and widespread. Emergent aquatic in rice field margins, restored wetland areas, and sloughs. *K. Duman 105* (DAV230821).

Typha latifolia L.

Common and widespread. Emergent aquatic in riparian sloughs, restored wetlands, and other perennially moist areas; more common than *Typha domingensis* and actively managed by the ranch to maintain open marsh habitat. *K. Duman 84* (DAV232913).

VERBENACEAE

Phyla nodiflora (L.) Greene

Common. Margins of restored wetland ponds and in vernaly moist areas in riparian woodland. *K. Duman 112* (DAV230823).

Verbena litoralis Kunth

Very common. Restored wetland margins and along sloughs in riparian woodland. *K. Duman 16* (DAV230508).

VISCACEAE

Phoradendron leucarpum (Raf.) Reveal & M.C.Johnst.

Uncommon parasite, growing primarily on *Populus* and *Salix* species throughout. *K. Duman 53* (DAV220727).

VITACEAE

Vitis californica Benth.

Common throughout. Riparian woodland. *K. Duman 15* (DAV230680).

ZYGOPHYLLACEAE

Tribulus terrestris L.

Uncommon. Gravelly disturbed ground by roads, mainly in the N section of the property. *K. Duman 135* (DAV232609).

LIMITING LIFE HISTORY STAGES IN THE ENDANGERED WETLAND PLANT *CIRSIUM HYDROPHILUM* VAR. *HYDROPHILUM* (ASTERACEAE)

ROSA S. SCHNEIDER^{1,2} AND KATHARYN E. BOYER

Estuary & Ocean Science Center and Department of Biology, San Francisco State University,
Tiburon, CA 94920

ABSTRACT

In addition to its high biodiversity, the California Floristic Province contains over 1600 rare taxa, including many endemics restricted to specific soil types and habitats. In the highly urbanized San Francisco Estuary, these narrow endemics face additional limitations from habitat destruction and modification, prompting an interest in their conservation and management. One such taxon, the Federally listed *Cirsium hydrophilum* (Greene) Jeps. var. *hydrophilum* (Suisun thistle), is restricted to two or three populations, and may face limitations beyond past habitat loss. In this study, we investigated life history limitations that may contribute to rarity in *C. hydrophilum* var. *hydrophilum*. We documented low seed set, high seed predation by beetle larvae, low localized wind dispersal of seeds, and possible inbreeding in smaller patches. Because seeds did not have a stringent germination requirement in the lab, however, restoration or introduction of new populations from seed is possible. Using seeds from larger source populations could increase success of reseeded, as could adding seeds to augment potentially low genetic diversity in existing smaller subpopulations. Further study is needed to understand the ecology of seed predators, the relative importance of seed set and seed germination in the field, and to confirm our potential finding of reduced genetic diversity and inbreeding. Though the causes and consequences of rarity may differ for each species, this study explores several research directions that could be productive for understanding other California endemic *Cirsium* and rare wetland endemics.

Key Words: brackish marsh, *Cirsium*, rare plant, rarity, San Francisco Estuary, Suisun Marsh, Suisun thistle, tidal wetland.

Rare species capture the attention of both naturalists and scientists; we are fascinated by their adaptations, and seek to know exactly why they are uncommon. On a more practical level, because many rare species are protected, understanding the biological and ecological processes driving their rarity is key to management and conservation, as well as to protecting their often-sensitive or limited habitats (Partel et al. 2005). With climate change, understanding what drives a species' rarity under current conditions is prerequisite for planning future conservation (Maschinski et al. 2006; Pacifici et al. 2015).

The term “rare” encompasses a diversity of meanings. In her seminal paper, Rabinowitz (1981) defined three axes of rarity along which species can be placed: geographic range, population size, and habitat specificity. These axes result in seven forms of rarity, with the eighth (widespread geographic range, large population size, and broad habitat specificity) applying to common species. Additionally, there are natural and anthropogenic drivers of rarity (Tibor and Dale 2001); naturally common species may become rare due to human activities, and species that are rare based on limited geographic range may become increasingly rare due to habitat alteration.

Given the many forms of rarity, scientists have investigated whether there are general properties of rare species that may be useful in conservation biology. Previous studies and meta-analyses have demonstrated that while some general trends exist, rarity is idiosyncratic (Fiedler 1987; Hegde and Ellstrand 1999; Gitzendanner and Soltis 2000). For example, Fiedler (1987) compared life history parameters and population dynamics for three rare and one common species of *Calochortus* (Liliaceae, Mariposa lilies). Despite some trends, not all traits were consistent across the three rare species compared to the common species. Though the common species was more likely to survive long enough to reproduce, some measures, including seed set per capsule, mean seed weight, and germination behavior were not different across species. Therefore, management of any particular species would depend on knowing its particular limitations.

Questions about rarity and its relationship to conservation and management are paramount in the California Floristic Province. Driven by a diverse geologic history, topography, and varied climate, the region is known for its high biodiversity and degree of endemism (Baldwin et al. 2012). California contains over 5300 native plant species and 6500 native plant taxa (32% of all U.S. taxa). Of these taxa, approximately 2300 are endemic to California (Stermer 2003; Jepson Flora Project 2020), and 1693 are classified as rare, threatened, or endangered within the state (California Native Plant Society

¹ San Francisco Bay National Estuarine Research Reserve, Tiburon, CA 94920

² Current address: California State Parks, Bay Area District, Petaluma, CA 94954. Rosa.Schneider@parks.ca.gov

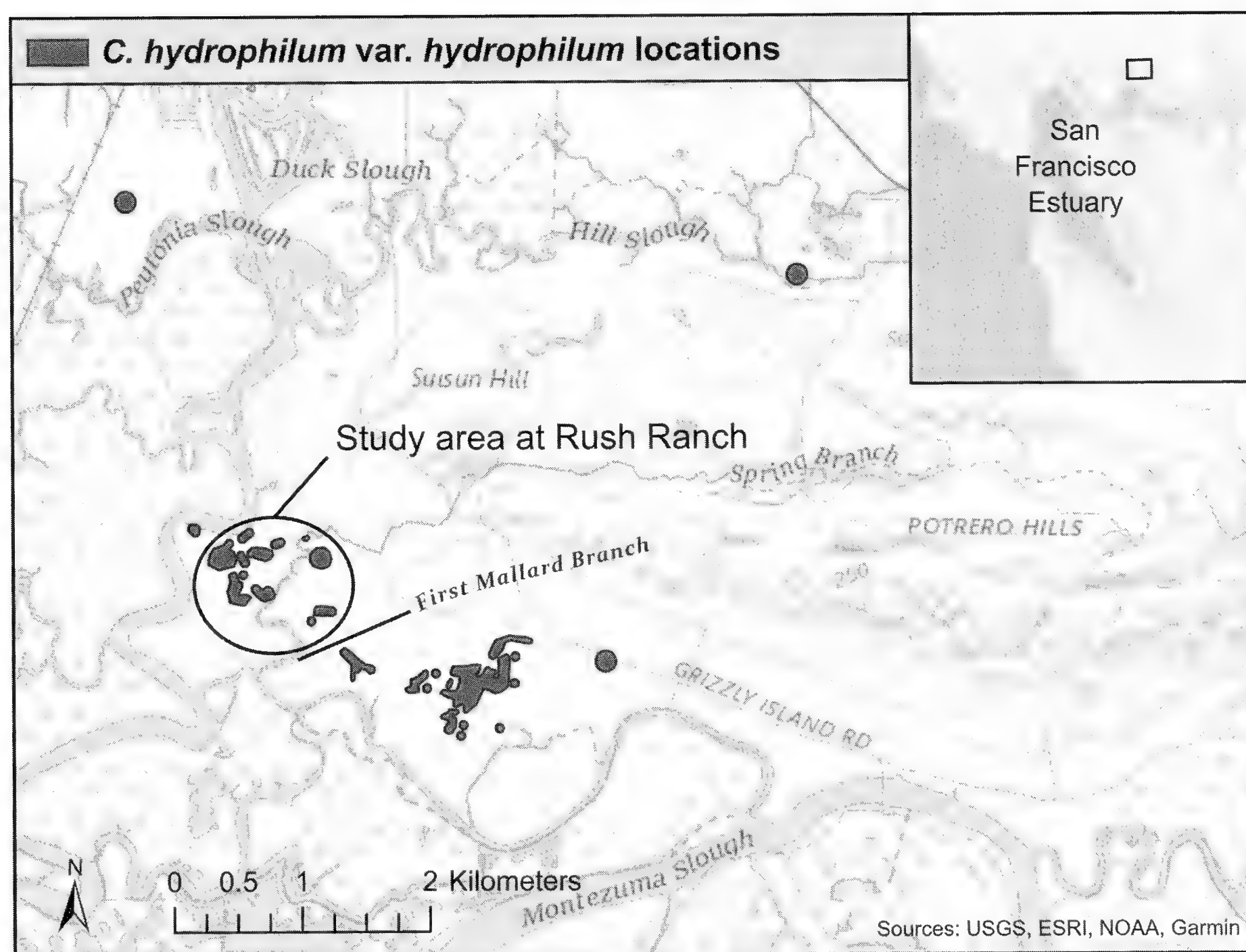


FIG. 1. Range map of *C. hydrophilum* var. *hydrophilum* (data from California Department of Fish and Wildlife 2020) indicating study area, and inset map showing location in San Francisco Estuary. Population at Peytonia Slough not observed since 1994.

2020). In this study, we take a closer look at one of California's 14 rare and endemic *Cirsium* taxa.

Cirsium ('true thistles') are in the Cardueae tribe, which also includes *Carduus*, *Centaurea*, and *Silybum*, among other genera. There are *Cirsium* endemic to North America, temperate Eurasia, and eastern tropical Africa, with the new world *Cirsium* forming a monophyletic group (Kelch and Baldwin 2003; Ackerfield et al. 2020a, 2020b). The New World *Cirsium* are found in a wide range of plant communities, including brackish marshes, seeps, dunes, meadows, swamps, forests, grasslands, deserts, and chaparral (Kelch and Baldwin 2003; Keil 2020). *Cirsium* are mainly monocarpic (flowering once) and either annual, biennial, or short-lived perennial, but can be polycarpic (flowering many times), establishing new taprooted rosettes via runner roots or from the caudex (Keil 2012).

A few highly invasive *Cirsium* (*C. vulgare* and *C. arvense*) have given the genus a bad reputation, but the majority of thistles found in North America are not invasive. In California, *Cirsium* contains endemic clade showing high habitat diversity across taxa and narrow geographic and habitat endemism within taxa (Kelch and Baldwin 2003; Ackerfield et al. 2020a). This natural rarity is often compounded by anthropogenic impacts to habitats (U.S. Fish and Wildlife Service 2010, 2014); 14 of the 38 native

Cirsium are rare, threatened, or endangered within the state (California Native Plant Society 2020).

In highly urbanized areas, such as the San Francisco Estuary (SFE), narrow endemics face impacts both from outright habitat destruction and ongoing alterations to ecosystems, including invasive species effects, changes in water salinity, sea level rise, and climate change (Schwartz et al. 2006; Seabloom et al. 2006; Callaway et al. 2007; Whitcraft et al. 2011; U.S. Fish and Wildlife Service 2013; Goals Project 2015). In Suisun Marsh (Northeast SFE), the endemic biennial *Cirsium hydrophilum* (Greene) Jeps. var. *hydrophilum* was once common along borders of channels and creeks in intact tidal marshes (Greene 1892). Since the 1930s, however, wetland diking and reclamation have greatly reduced the area of intact tidal marsh, and *C. hydrophilum* var. *hydrophilum* is now a Federally listed endangered species with only three populations documented in western Suisun Marsh over the last 25 yr (U.S. Fish and Wildlife Service 2013; Fig. 1). While negative impacts of habitat destruction and alteration on *C. hydrophilum* var. *hydrophilum* and the SFE flora are in general well-known, monitoring and research on this species have been limited, and intrinsic and ecological limitations have not been investigated (Goals Project 1999; Fiedler et al. 2007; U.S. Fish and Wildlife Service 2009, 2013). These limitations could prevent *C. hydrophilum* var. *hydro-*



FIG. 2. Photos of *C. hydrophilum* var. *hydrophilum* inflorescence (left), plants (upper right) and brackish marsh habitat and seed trap experiment (lower right).

philum from spreading into additional suitable habitat, and may compound the effects of invasive species, climate change, and localized disturbance events (Fiedler et al. 2007; U.S. Fish and Wildlife Service 2009, 2013). Furthermore, restoration efforts planned for Suisun Marsh lack information on *C. hydrophilum* var. *hydrophilum*'s biology and ecology that is needed to adequately consider this species' requirements. Thus, the aim of our study was to determine limiting stages in *C. hydrophilum* var. *hydrophilum*'s life history, particularly with respect to habitat variables and ecological context.

Based on past studies of other *Cirsium* (Zedler et al. 1983; Louda and Potvin 1995; Herr 2000; Maron et al. 2002; Hillman 2007; Powell et al. 2011) and an agency report on our focal species (U.S. Fish and Wildlife Service 2009), we hypothesized that low seed set, high seed predation, and low seed dispersal are limiting factors during important life history stages in *C. hydrophilum* var. *hydrophilum*. We were particularly interested in determining environmental variables that correlate with seed set, predation, dispersal, and germination, to be able to make specific recommendations for restoration and management of this species. In doing so, we intended to help frame research on other rare wetland endemic species.

MATERIALS AND METHODS

Study Site

Rush Ranch (38°12'31.7"N, 122°1'31.9"W) contains 425 ha of brackish tidal marsh within a 2000 ha preserve that is part of the National Estuarine Research Reserve System. Like the surrounding

Suisun Marsh and other SFE wetlands, Rush Ranch is invaded by *Lepidium latifolium* L. (Brassicaceae, perennial pepperweed), particularly during years with ample rainfall (Whitcraft et al. 2011; Kelso et al. 2020). However, it retains relatively large areas of undiked, intact tidal marsh and is home to several rare, threatened, and endangered species, including *Laterallus jamaicensis coturniculus* Ridgway (California black rail), *Rallus longirostris obsoletus* Ridgway (California Ridgway's rail), *Reithrodontomys raviventris* Dixon (salt marsh harvest mouse), *Chloropyron molle* subsp. *molle* (A.Gray) A.Heller (Orobanchaceae, soft bird's beak), *Symphyotrichum lentum* (Greene) G.L.Nesom (Asteraceae, Suisun Marsh aster), and the largest extant population of *C. hydrophilum* var. *hydrophilum* (Whitcraft et al. 2011; Goals Project 2015). This study took place within the First Mallard Branch area, which contains several large patches of *C. hydrophilum* var. *hydrophilum* (Figs. 1, 2).

Seed Set and Predation

Seed set was quantified by bagging post-bloom inflorescences to prevent dispersal, followed by later enumeration in the lab. In late July 2011, five discrete patches of *C. hydrophilum* var. *hydrophilum* spread evenly throughout the study area and more than 100 m apart were chosen. At each site, six recently wilted inflorescences were covered in cotton muslin bags with drawstrings (called "sand sacs," purchased from local bait stores, dimensions 6.5 cm x 8 cm) (per Surles and Kok 1978). Additionally, to examine whether *C. hydrophilum* var. *hydrophilum* flowers can self-fertilize within an inflorescence, ten unopened inflorescences were also bagged to prevent wind and

insect pollination. Bagged inflorescences were collected once the seeds were ripe, as evidenced by the presence of seeds and pappus inside the bags 2 wk later. Insects observed visiting flowers were collected by hand and using a sweep net, and stored in ethanol for later identification.

In July 2012, to further explore factors correlated with seed set, we identified six discrete patches of *C. hydrophilum* var. *hydrophilum* spread throughout the study area and separated by at least 175 meters. At each site, patch dimensions were determined, individual plants were counted, and inflorescences per plant were counted for a subset of plants. Five post-bloom inflorescences were randomly selected at each site and covered with muslin bags for later collection, as in 2011. Finally, soil cores (one per site; 5 cm diameter) were taken using a PVC corer with a sharpened edge and separated into 0–2 cm and 2–6 cm depth to determine soil moisture, salinity, and organic content.

In the lab, each seedhead was carefully dissected, and fully formed seeds were counted. Evidence of seed predation (presence of insect larvae or their frass) was noted. Arthropods were described and counted, and a subset were preserved in ethanol for identification.

Seed Dispersal

Wind. To examine seed dispersal by wind, linear transects originating at the edge of *C. hydrophilum* var. *hydrophilum* patches were established at three sites. Seed traps made of plastic funnels (diameters = 8.25 cm, 14.5 cm, and 17 cm) attached to mesh bags were mounted on PVC (per Cottrell 2004) and installed at 1 m, 3 m, and 8.5 m from the patch edge in each of the four cardinal directions (Fig. 2). Vegetation hanging directly above traps was clipped to allow seeds to fall vertically into the traps. To ensure that a constant proportion of the area was sampled at each distance from the patch, funnel opening sizes increased with distance. Traps were installed mid-July 2012, as seeds were beginning to disperse, and were checked every 2 wk until no further seeds were trapped (8 wk later, in mid-September). Seeds were counted and classified as fully formed (plump with a thick seed coat) or non-viable (flattened with a thin seed coat), and presence or absence of pappus was recorded.

Hydrochory. To examine the potential for dispersal by water, *C. hydrophilum* var. *hydrophilum* seeds were placed in 28-L tanks containing water of 0, 5, or 10 ppt salinity (50 seeds per tank, $n = 4$, for a total of 12 tanks) in a randomized block design. Seeds were collected from throughout the study area in August 2011 and stored in the lab without cold scarification or other treatments. Aquarium air bubblers were used to break surface tension, simulating water movement in the field. Salinity levels were obtained by dissolving Instant Ocean Sea Salts

(Spectrum Brands, Atlanta, GA) in tap water, and were adjusted to account for evaporation. On Days 1, 2, 4, 8, 16, 19, 21, and 23, the number of seeds floating and number of seeds germinated were recorded. On Days 1, 2, 4, 8, and 16, a subset of seven seeds from the bottom of each tank was removed, rinsed with freshwater, and placed in Petri dishes with moistened filter paper to quantify subsequent germination.

Seed Germination

Salinity experiment. Seed germination was tested at six salinity levels (0, 5, 10, 15, 20, and 25 ppt), ranging from fresh conditions to that of soil salinity measured beneath plants in October 2011 (mean = $19.7 \text{ ppt} \pm 6.3 \text{ ppt}$ [95% CI]; Schneider 2013). In the lab, 10 seeds collected in August 2011 from a mixture of sites were placed in a Petri dish lined with filter paper ($n = 6$, Kuhn and Zedler 1997). Four mL of salt solution made from Instant Ocean Sea Salts and deionized water were added to each dish, which was enough to keep seeds in contact with solution, but not enough to submerge them. Dishes were covered to prevent desiccation and discourage mold growth, and placed randomly in a temperature-controlled environmental chamber at 19°C on a diurnal cycle of 12 hr light: 12 hr dark, simulating fall light and temperature levels in Suisun Marsh (NOAA 2004). Water salinities in the dishes were checked every 2 to 3 d and adjusted to account for evaporation. Seed germination was recorded weekly for 4 wk.

Cold stratification. To examine whether *C. hydrophilum* var. *hydrophilum* seeds require or benefit from cold stratification, seeds collected from a mixture of sites in August 2011 were placed in Petri dishes (five seeds per dish, $n = 10$) on top of moistened filter paper, and placed in a refrigerator (5°C) for 2 wk (Emery 1988; Diggory and Parker 2011). After this time, filter paper and water were changed to discourage mold growth. Petri dishes were transferred to an environmental chamber along with control dishes of non-stratified seeds (not pre-soaked at 5°C or at room temperature). Temperature and light were controlled as above and germination was recorded weekly for 2 wk.

Germination differences by site. All seeds from each seedhead collected in July 2012 were germinated separately in one or more Petri dishes ($n = 5$ seedheads per site). A maximum of 21 seeds per dish were placed on filter paper moistened with deionized water and kept under the temperature and light conditions described above for 2 wk.

Statistical Analyses

All analyses were conducted in R Studio Version 1.1.453 (R Studio, PBC, Boston, MA). Both seed set and seed germination of field-collected seeds were compared across sites using a one-way ANOVA. To

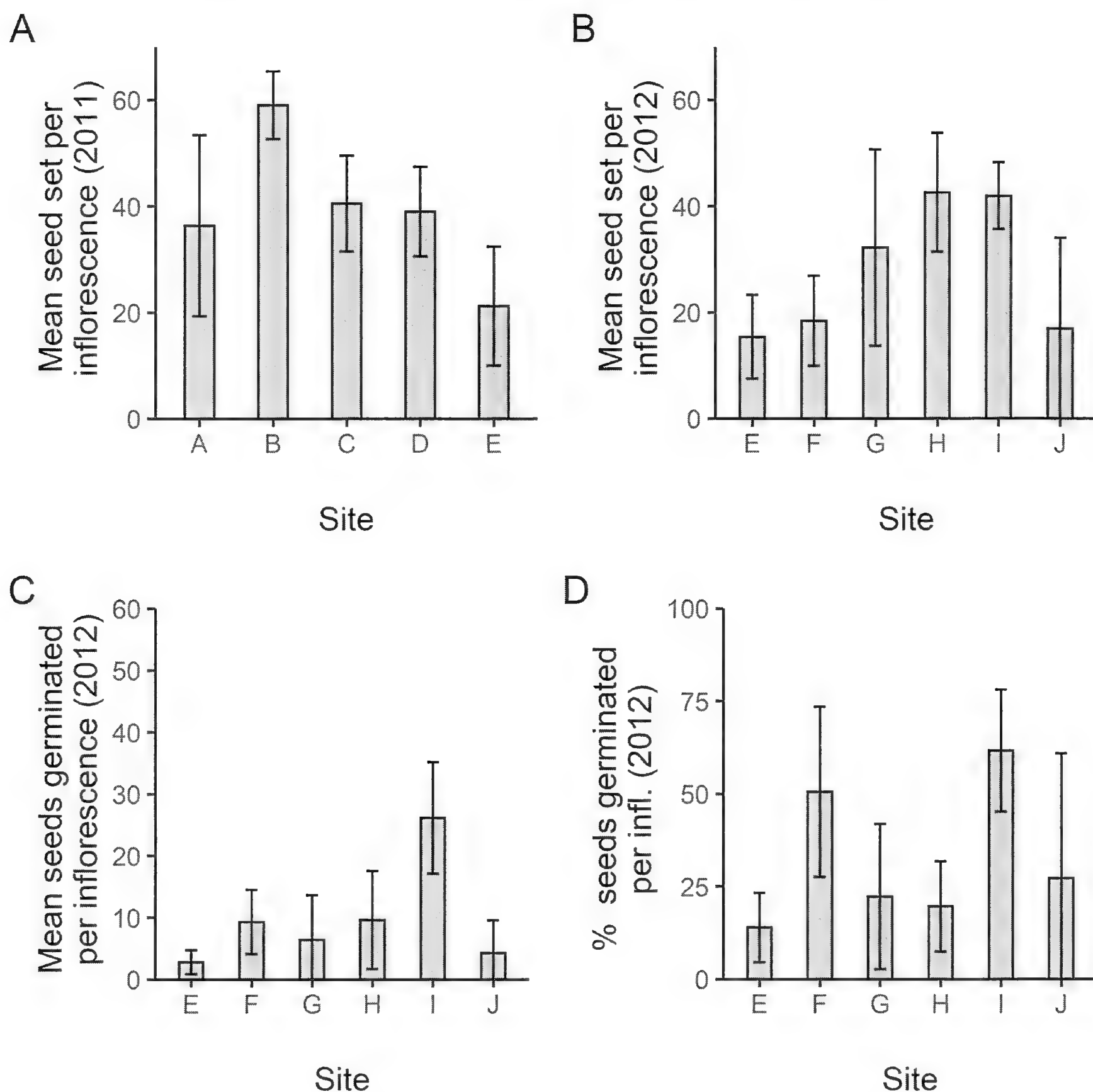


FIG. 3. (A) Mean seed set by site in 2011. (B) Mean seed set by site in 2012. (C) Mean seeds germinated per inflorescence by site in 2012. (D) Mean percent germination per inflorescence by site in 2012, $n = 6$ inflorescences per site (2011), $n = 5$ inflorescences per site (2012). Letters indicate pairwise differences across sites ($P < 0.05$). Error bars show 95% confidence intervals. Site E was sampled in both years.

determine which environmental variables correlated with seed set and seed germination between sites, all variables were plotted and those with visual trends were further investigated using linear regression. The relationship between the number of larvae in seed-heads and seed set was also examined using linear regression. A t-test was used to compare seed set between seedheads with and without evidence of predation.

After summing seed trap data across dates and cardinal directions, a seed dispersal curve was constructed to examine how seeds trapped per square meter changed with distance from the patch edge.

Because data on seed flotation and germination in tanks could not be adequately transformed to meet assumptions of normality, 95% confidence intervals were compared to examine the effect of salinity treatment. Similarly, following flotation, Petri dish seed germination data could also not be adequately transformed, thus 95% confidence intervals were compared.

For the salinity germination experiment, effect of salinity was examined with a Kruskal-Wallis test. Effect of cold stratification on germination was examined using a Wilcoxon rank-sum test.

RESULTS

Seed Set and Seed Germination of Field-collected Seeds

Across all sites in 2011 and 2012, mean seed set per inflorescence was 33.7 seeds ($SD = 18.2$; Fig. 3A, B). Based on an average of 90 flowers per inflorescence, mean percent seed set was 37.4% ($SD = 20.2\%$). Of all seeds collected in 2012, 34.2% germinated in Petri dishes (Fig. 3D).

Seed production by inflorescences with unopened flowers that had been bagged showed that flowers are able to self-fertilize within an inflorescence. However, compared to unbagged inflorescences (see above), mean seed set in self-pollinated inflorescences was low, at 1.2 seeds per inflorescence ($SD = 2.3$).

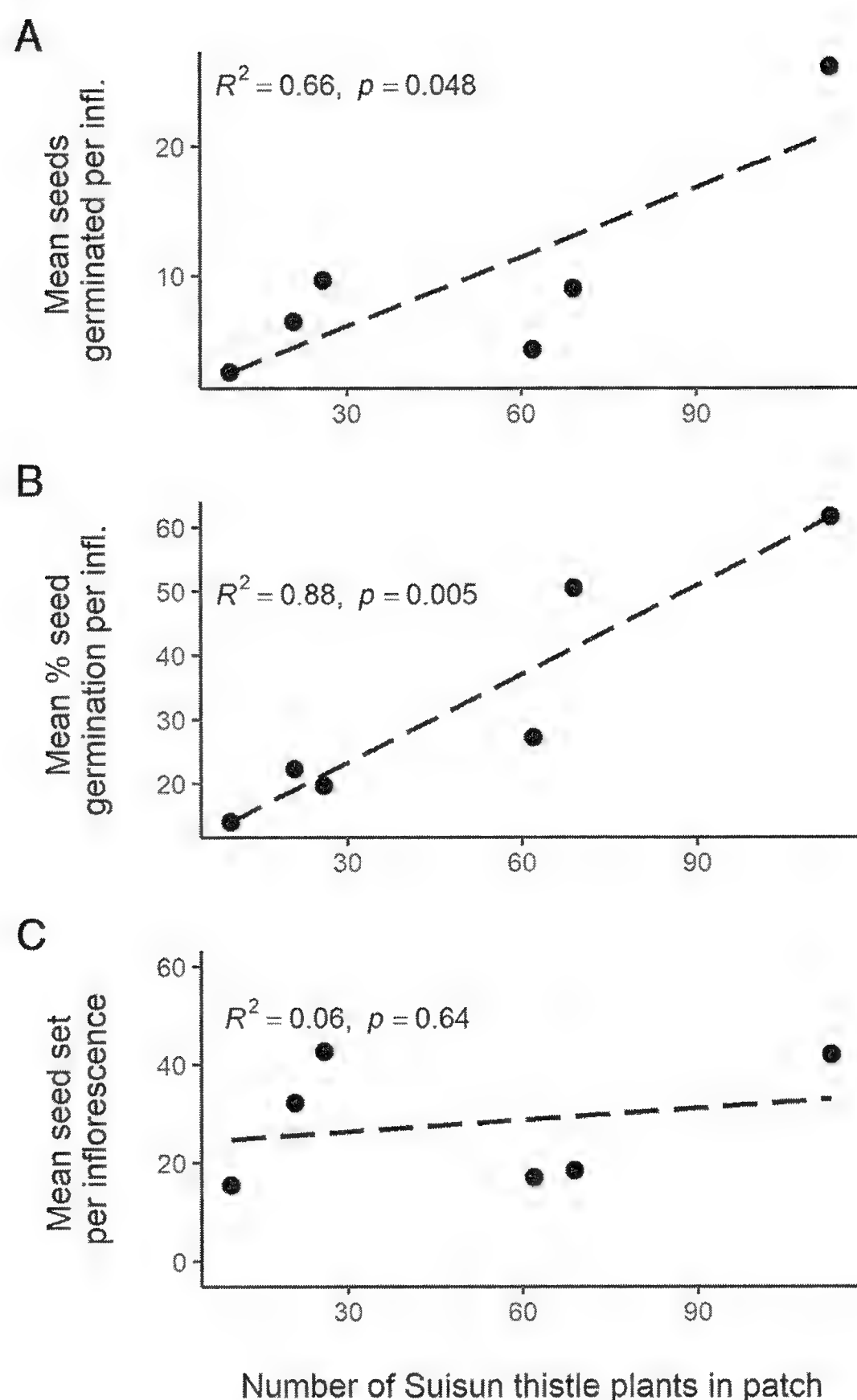


FIG. 4. Relationship between the number of *C. hydrophilum* var. *hydrophilum* plants per patch and (A) mean number of seeds germinated per inflorescence, (B) percent of seeds germinated per inflorescence, and (C) number of seeds per inflorescence.

Nonetheless, these seeds were highly viable, with 91% germinating in fresh water.

In 2011, seed set differed significantly by site ($F_{4,23} = 5.69, P = 0.002$, Fig. 3A). In 2012, there was no overall site effect on seed set ($F_{1,28} = 1.70, P = 0.20$; Fig. 3B); however, both number of seeds germinated and percent seeds germinated per inflorescence varied significantly by site (number germinated, $F_{5,22} = 4.75, P = 0.004$, Fig. 3C; percent germinated, $F_{5,22} = 3.72, P = 0.01$, Fig. 3D).

Number of *C. hydrophilum* var. *hydrophilum* plants per patch was significantly positively correlated with both mean number of seeds germinated per inflorescence ($R^2 = 0.66, F_{1,4} = 7.88, P = 0.048$, Fig. 4A) and percent of seeds germinated per inflorescence ($R^2 = 0.88, F_{1,4} = 29.81, P = 0.005$, Fig. 4B), but not with the number of seeds per inflorescence ($R^2 = 0.06, F_{1,4} = 0.26, P = 0.64$, Fig. 4C). No soil properties were significantly correlated with seed set or seed germination (data given in Appendix 1).

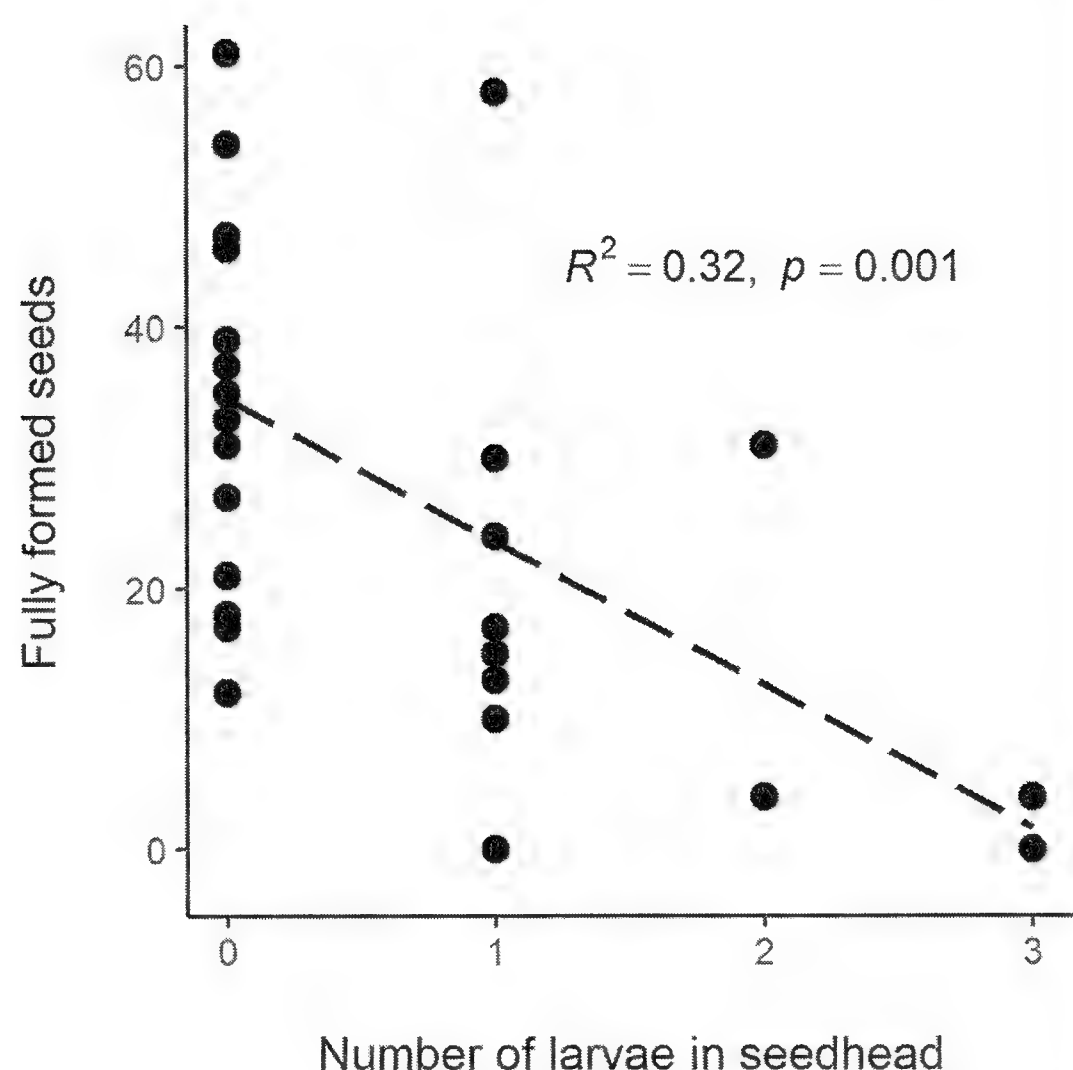


FIG. 5. Relationship between number of *Lasioderma haemorrhoidale* larvae and number of *C. hydrophilum* var. *hydrophilum* seeds per seedhead (2012).

Seed Predation

Of all seedheads collected in 2011 and 2012, 31% showed evidence of predation by beetle larvae later identified as *Lasioderma haemorrhoidale* (family Anobiidae, order Coleoptera). In *C. hydrophilum* var. *hydrophilum*, larvae were observed eating seeds and nesting in tissue of the receptacle. Seedheads with evidence of predation (i.e., larvae or their frass) contained a mean of 23.1 seeds (95% CI = ± 9.5 seeds), while those without evidence of predation contained approximately 40% more, with a mean of 38.5 seeds (95% CI = ± 5.0 seeds); this difference was significant ($t = 2.99, df = 27.64, P = 0.0058$). In 2012, when larvae were counted in each seedhead, the number of seeds was significantly negatively correlated with the number of larvae ($R^2 = 0.32, F_{1,28} = 13.25, P = 0.001$; Fig. 5). Other insects collected are described in Table 1.

Seed Dispersal

Wind. Seed rain followed a leptokurtic distribution (by definition, a sharp peak around the mean, with a longer tail compared to a normal distribution), with most seeds trapped closest to the patch edge (Fig. 6). Both seeds (often with pappus detached) and pappus were often observed directly below parent plants, i.e., at 0 m from the patch edge. Seed dispersal varied by cardinal direction, with higher dispersal in the north and east directions (55% and 45% of all seeds trapped, respectively) and no seeds trapped in the south or west direction. None of the trapped seeds had pappus attached. We did not observe elaiosomes (fleshy, lipid and protein-rich

TABLE 1. Insects collected from *C. hydrophilum* var. *hydrophilum* in the field (from living inflorescences) and in the lab (during seedhead dissection).

Collected from	Order	Family	Species	Potential role	Date collected
Inflorescence	Coleoptera	Meloidae	<i>Nemognatha lutea</i>	phytophage	7.1.2011
Inflorescence	Hemiptera	Miridae	<i>Lygus</i> sp.	herbivore	7.13.2011
Inflorescence	Hymenoptera	Apidae	<i>Bombus vosnesenskii</i>	pollinator	7.1.2011
Inflorescence	Hymenoptera	Apidae	<i>Ceratina</i> sp.	pollinator	7.1.2011
Inflorescence	Hymenoptera	Apidae	<i>Diadasia bituberculata</i>	pollinator	7.13.2011
Inflorescence	Hymenoptera	Megachilidae	<i>Osmia</i> sp.	pollinator	7.1.2011
Seedhead	Coleoptera	Anobiidae	<i>Lasioderma haemorrhoidale</i>	observed seed predator	12.23.2010, 8.2011, 9.11.2012
Seedhead	Coleoptera	Anthicidae			12.23.2010
Seedhead	Coleoptera	Chrysomelidae	<i>Chaetocnema irregularis</i>	phytophage	12.23.2010
Seedhead	Coleoptera	Curculionidae	<i>Anthonomus ater</i>	phytophage	12.23.2010
Seedhead	Coleoptera	Curculionidae	<i>Sibinia maculata</i>	phytophage	12.23.2010
Seedhead	Coleoptera	Dermestidae			8.29.2011
Seedhead	Hemiptera	Miridae	<i>Lygus</i> sp.	herbivore	8.12.2011
Seedhead	Hymenoptera	Bethylidae			12.23.2010
Seedhead	Psocodea	Psocidae			8.28.2011

protuberances) on the seeds, which, if present, would have implied some dispersal by ants.

Hydrochory. On Day 1 (1 d after the experiment began), only 23.5% (SD = 21.2%) of seeds placed in tanks were floating; on Day 2, 19.8% (SD = 21.2%) were floating (Fig. 7A). Seeds generally floated best in fresh water, though variation was high. On Day 8, nearly all seeds had sunk to the bottom of the tanks, coincident with the first observed germination (Fig. 7B). While in the tanks, seeds in 0 ppt salinity water germinated at higher rates than in the 10 ppt treatment, with the 5 ppt treatment showing intermediate rates, although an average of only 10 seeds

(out of 50 per tank) germinated by the end of the experiment on Day 23 (Fig. 7B). However, the subset of sunken seeds removed on Days 1, 2, 4, 8, and 16 and placed in Petri dishes germinated at very high rates (95%, SD = 8.3%) regardless of salinity treatment or day removed (Fig. 7C).

Seed Germination

Mean percent germination was not significantly different between cold-stratified and non-cold stratified treatments ($W = 44$, $P = 0.66$). Across both treatments, germination was 84% (95% CI = $\pm 7\%$). In the salinity germination experiment, salinities in the Petri dishes increased despite repeated replacement of water; treatments are thus presented as ranges. There was a significant negative effect of salinity on seed germination (Kruskal-Wallis $\chi^2 = 23.30$, $df = 5$, $P < 0.001$) with the percentage germinating declining from 32% at 0 ppt to $<3\%$ at salinities greater than 20 (Fig. 8).

DISCUSSION

Though *C. hydrophilum* var. *hydrophilum*'s rarity is largely due to its narrow endemism, widespread habitat alteration has reduced its geographic range and overall population numbers to the point where life history limitations may be critically important. We quantified reproductive output at various life history stages, documenting that low seed set, high levels of predation, low localized wind dispersal of seeds, and highly variable seed germination are likely further increasing rarity in this taxon. More specifically, limited wind dispersal may serve to reinforce or even decrease its small geographic range, while low seed set, high seed predation, and variable seed germination likely limit local abundances. In aggregate, these limitations may be creating increasingly isolated subpopulations that fail to reestablish

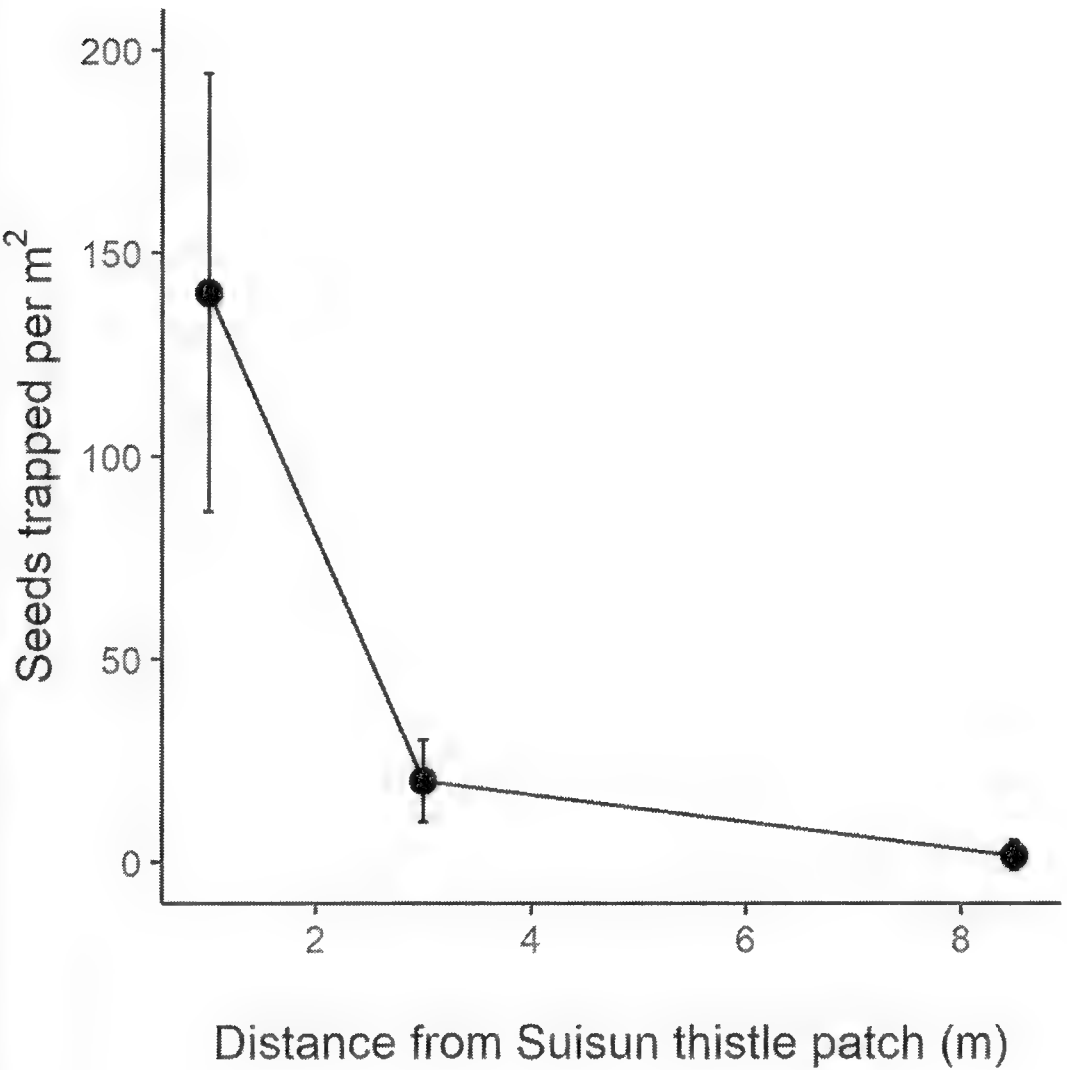


FIG. 6. Seeds trapped per m² as a function of distance from *C. hydrophilum* var. *hydrophilum* patch edge at three sites during summer 2012. Error bars show 95% confidence intervals.

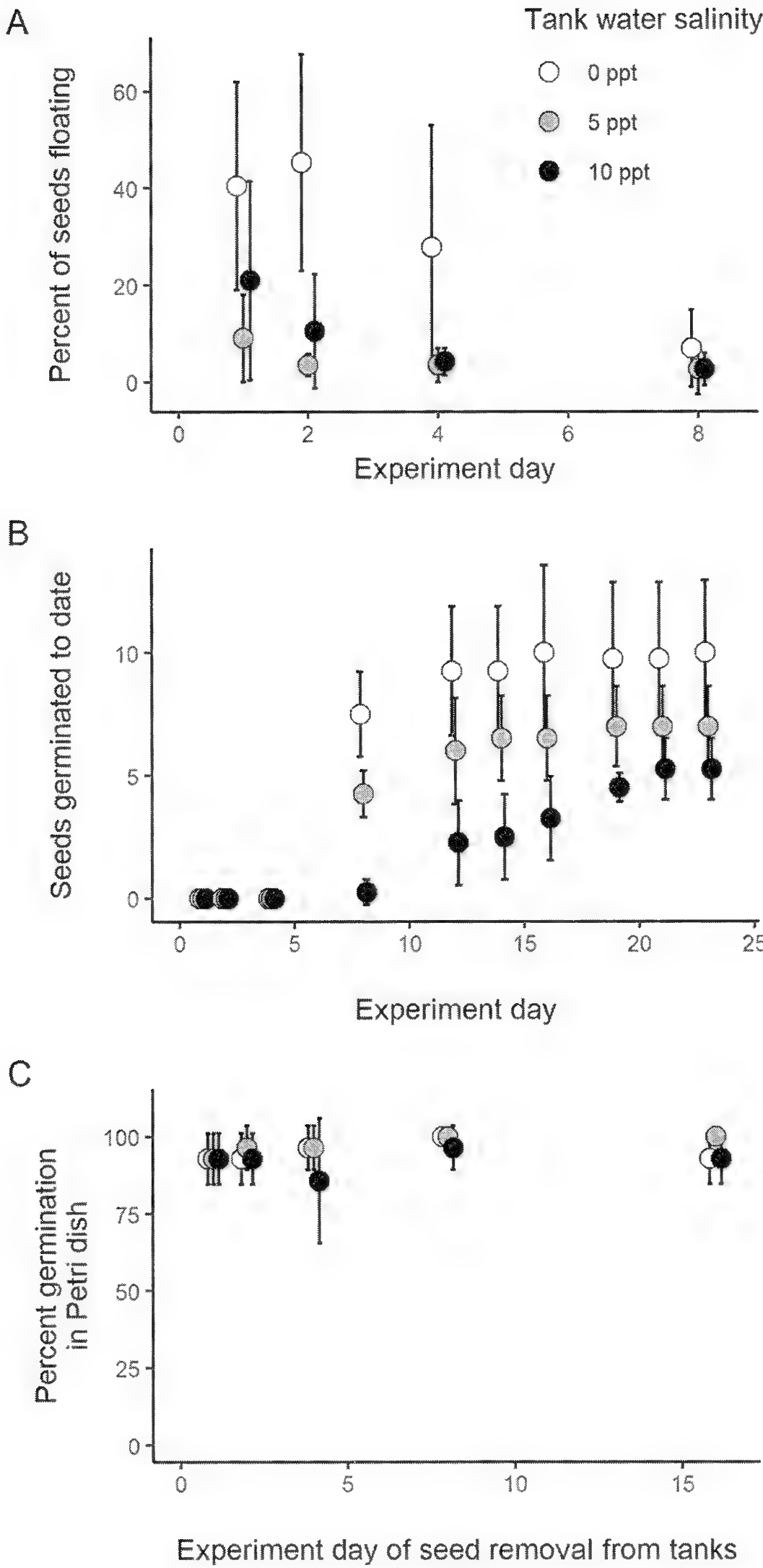


FIG. 7. Hydrochory experiment. (A) Percent of seeds floating on the surface of tank water over time. (B) Number of seeds germinated in tanks over time. (C) Percent seed germination in Petri dishes after removal from tanks on different days. Error bars show 95% confidence intervals; n = 4.

following localized extinction events, further reducing its geographic range. Conversely, as detailed below, increasing local subpopulations sizes and establishing new populations through seed addition could prevent further restriction of this taxon's geographic range and continued persistence in a changing environment.

Seed Set and Seed Germination of Field-collected Seeds

Powell et al. (2011) measured seed production in several native California *Cirsium* as well as the

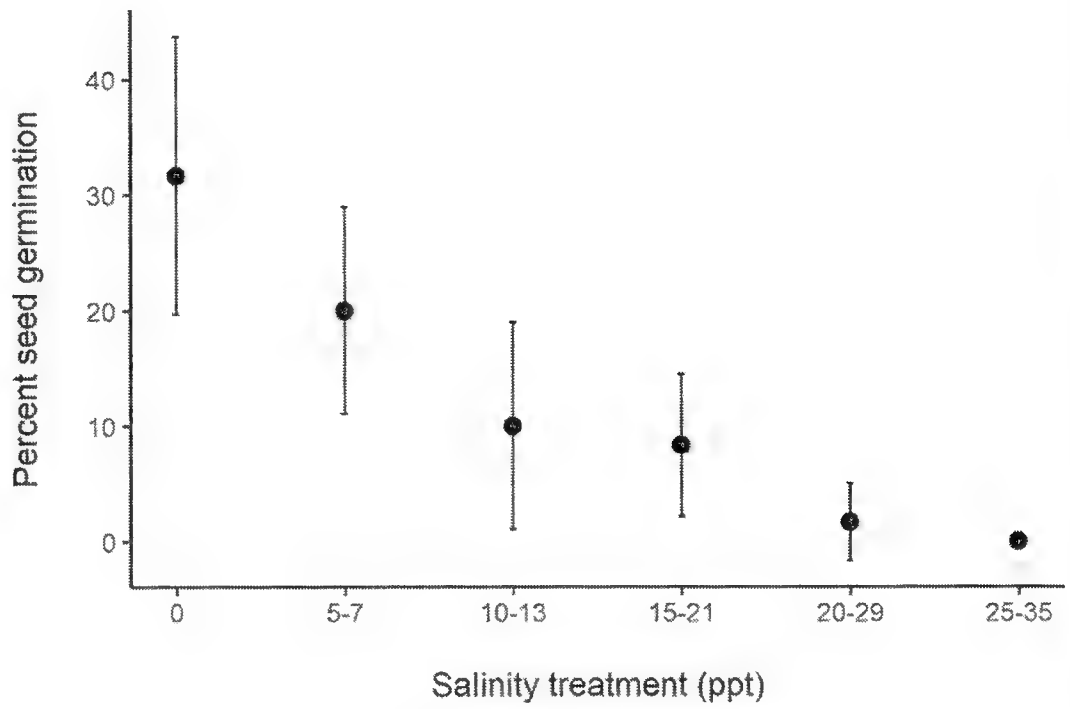


FIG. 8. Mean percent seed germination by salinity treatment. Error bars show 95% confidence intervals; n = 6.

invasive bull thistle, *Cirsium vulgare* (Savi) Ten. Of all taxa studied, seed set was lowest in *Cirsium fontinale* Jeps. var. *fontinale*, a narrow endemic confined to serpentine seeps in San Mateo County. Zedler et al. (1983) found even lower seed set in *Cirsium rhotophilum* S.F. Blake, a state-listed (threatened) narrow endemic found in sand dunes of San Luis Obispo and Santa Barbara Counties.

Seed set in *C. hydrophilum* var. *hydrophilum* was lower than all *Cirsium* congeners examined by Powell et al. (2011) (Fig. 9). Mean germination of 34% reduced effective reproductive output from an average of 34 to 10 seeds per inflorescence. While there was no relationship between the number of plants in a patch and number of seeds produced, the positive correlation between plants per patch and seed germination indicates potential inbreeding depression in smaller patches (Menges 1991; Heschel and Paige 1995). This may be both a cause and consequence of rarity; i.e., reduced genetic variation may be a result of reduced population size.

Seed Predation

Seed predation in *Cirsium* has been widely documented. Louda and Potvin (1995) and Maron et al. (2002) used exclusion experiments to show that insect damage limited seed production, seedling recruitment, and juvenile plant densities in their respective study species, *Cirsium canescens* Nutt. and *Cirsium occidentale* var. *occidentale* (Nutt.) Jeps. In *C. rhotophilum*, insect predation caused a loss of at least 25% of seeds (Zedler et al. 1983). In the upper Great Lakes, Havens et al. (2012) showed that seed predation by the non-native biocontrol weevil *Larinus planus* decreased population growth of endangered *Cirsium pitcher* Torr. & A. Gray by 10–12%, reducing predicted time to extinction by nearly half in certain populations. Seed predation by *Rhinocyllus conicus*, a weevil introduced to control nuisance thistles, has negatively impacted several native *Cirsium* in the Midwest (Louda et al. 1997, 2005). Larvae of this weevil have been reared

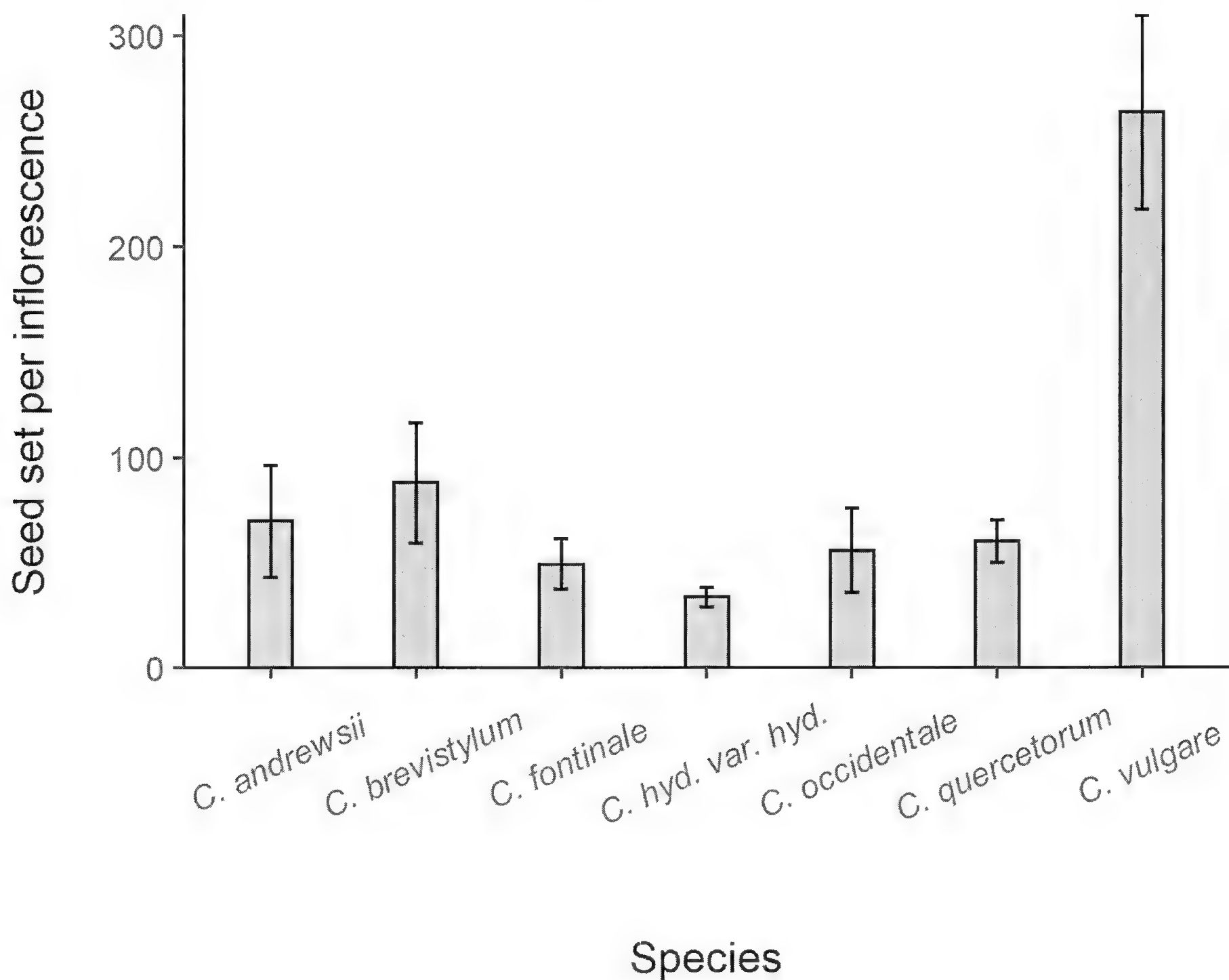


FIG. 9. Seed set in various *Cirsium* taxa. Except for *C. hydrophilum* var. *hydrophilum*, data are from Powell et al. 2011, whose work examined native and invasive *Cirsium* around the San Francisco Bay Region. Error bars show 95% confidence intervals; n between 32 and 67 for Powell et al. data; n = 58 for *C. hydrophilum* var. *hydrophilum*.

from many California *Cirsium*, including *C. hydrophilum* var. *hydrophilum* (Turner et al. 1987; Herr 2000). Herr (2000) documented seed predation impacts of *R. conicus* on *C. hydrophilum* var. *hydrophilum*'s conspecific variety, *Cirsium hydrophilum* var. *vaseyi* (A. Gray) J.T. Howell, but hypothesized that a mismatch between timing of weevil oviposition and seed formation minimizes predation impacts.

In this study, we found that seed predation by *L. haemorrhoidale* is significantly reducing *C. hydrophilum* var. *hydrophilum*'s reproductive output, lowering the number of seeds per seedhead by an average of 40%. In a related study which examined effects of invasive *Lepidium latifolium* on *C. hydrophilum* var. *hydrophilum*, even higher predation levels were observed where *C. hydrophilum* var. *hydrophilum* was growing within a matrix of dense *L. latifolium* (Schneider 2013). Native to the Mediterranean, *L. haemorrhoidale* is commonly found in *Centaurea solstitialis* L. (Asteraceae, yellow starthistle) and *Centaurea calcitrapa* L. (Asteraceae, purple starthistle) in California, and was reared from a seedhead of the rare *Cirsium fontinale* var. *campylon* in 1982 (White 1990; Woods 1999). *C. solstitialis* is widespread along the marsh-terrestrial ecotone and in the uplands at Rush Ranch, and may be providing a large source population of these beetles.

Seed Dispersal

The leptokurtic shape of *C. hydrophilum* var. *hydrophilum*'s dispersal curve is common to most species (Levin and Kerster 1975), confirming that localized dispersal by wind is minimal. Though seeds were only trapped in the direction of regional prevailing winds, their pappus does not appear to play much of a role in dispersal, as it was not attached to any trapped seeds and was often observed in aggregations directly below parent plants. However, this study only measured short-distance dispersal; though rare, long distance dispersal events can be important in establishing new patches or populations (Willson 1993; Cain et al. 1998).

Limited wind dispersal may be an evolutionary adaptation to staying in suitable habitat, and thus a consequence of *C. hydrophilum* var. *hydrophilum*'s narrow endemism. Alternatively, it may be a cause of rarity; i.e., if pappus did not readily detach, perhaps this species would have colonized and adapted to a wider range of habitats. In either case, low seed dispersal may lead to genetic isolation between patches. For rare species, propagule flow between patches can be important in maintaining genetic diversity, and in rescuing sink populations that are small or in less suitable habitat (Brown and Kodric-Brown 1977; Craddock and Huenneke 1997).

Hydrochory is common in wetland plants (Nilsson et al. 2010) and was examined in *Cirsium vinaceum* Wooton & Standl., a New Mexico wetland endemic (Craddock and Huenneke 1997). The authors found that large numbers of seeds traveled and remained viable for up to 280 m in streams; it is therefore possible that *C. hydrophilum* var. *hydrophilum* may also disperse by water. Though hydrochory was not measured *in situ*, experimental data suggest that dispersal by water may also be a limiting life history stage, as seed flotation levels were low after just 2 d in 5 ppt and 10 ppt salinity water. Because seeds that did not germinate in tanks remained viable throughout the experiment, however, seeds could potentially be carried by water in channels to new locations. Field studies would be needed to investigate whether seeds indeed reach channels and are carried back up onto the marsh. Whether by wind or water, there is likely at least occasional long-distance dispersal of this species, given its past and present distribution in Suisun Marsh.

Seed Germination

An inverse germination response to salinity is not surprising for a brackish marsh species (Greenwood and MacFarlane 2006). Lack of germination in the 25–35 ppt treatment indicates an upper salinity tolerance. Soil salinities in and above this range were observed in October 2011 beneath *C. hydrophilum* var. *hydrophilum* plants (Schneider 2013); thus, germination may occur later in the season with freshwater input from rain.

The cold stratification experiment confirms that *C. hydrophilum* var. *hydrophilum* seeds do not have a stringent germination requirement for cold temperatures. This supports our observations that seeds germinate as early as September in the field, but also means that early germinating seedlings must survive low light and temperatures throughout the winter.

Even within suitable existing habitats, however, space and light for seedling germination may be limited by dense marsh vegetation. Our observations suggest that openings for seed germination are often generated by soil disturbance resulting from the fall of senescing rosettes. This has also been observed in the habitat of *Cirsium fontinale* Jeps. var. *obispoense* J.T. Howell, where dense grass cover appears to inhibit seed germination except where decomposing thistle leaves create an opening (Chipping 1994). *C. hydrophilum* var. *vaseyi* is also a narrow endemic, found only on serpentine seeps of Mount Tamalpais, Marin County, California. Seedling density beneath parent plants is extremely high, but unlike in the brackish marsh, competition for light and space in serpentine outcrops is relatively low and this dispersal strategy may not lead to reduced reproductive output in that setting.

Management Implications

Because *C. hydrophilum* var. *hydrophilum* seeds do not have unusual germination requirements, restoration or introduction of new populations from seed is possible. Their inverse germination response to salinity, however, suggests that seed introduction should be timed to the rainy season when soil salinity is lower. Using seeds from larger source patches or subpopulations could increase success of reseeding, as could combining seeds from a variety of sources. Additionally, seeds from larger subpopulations could potentially be used to augment possible low genetic diversity in existing smaller subpopulations. Though preserving local lineages can be important for rare species populations that are geographically disparate, all known occurrences of *C. hydrophilum* var. *hydrophilum* are separated by no more than 3 to 4 km, with the largest patches within 1 km of each other. More broadly, in light of climate change, establishing new populations on the more freshwater end of *C. hydrophilum* var. *hydrophilum*'s current brackish marsh range may be one strategy to help this species migrate up the estuary, as increased salinity and drought frequency and intensity are expected to facilitate brackish marsh to salt marsh transition (Parker et al. 2011; Goals Project 2015; Parker and Boyer 2019).

Capitalizing on natural disturbance events, including the occasional, intermittent feral pig soil disturbance observed at Rush Ranch, could also increase success of restoration efforts, as these are high light environments in which seeds would have an increased chance of germination and survival. Such seedbeds could be mapped and monitored to favor colonization by *C. hydrophilum* var. *hydrophilum* and other native species. However, based on limited wind dispersal, we should not expect new subpopulations to naturally reseed into nearby suitable habitat. As an overall recommendation, controlling *L. latifolium* in the vicinity of *C. hydrophilum* var. *hydrophilum* could increase the thistle's reproductive output (Schneider 2013).

CONCLUSIONS AND FUTURE DIRECTIONS

In this study, we examined reproductive output in the wetland endemic *C. hydrophilum* var. *hydrophilum* in order to identify limiting life history stages that may further contribute to its rarity. Our data demonstrate that low levels of seed set are compounded by seed predation from an introduced anobiid beetle, low localized wind dispersal of seeds, and salinity-dependent and highly variable seed germination.

In addition to the management implications discussed above, this study raises several new hypotheses. Based on the finding that seed output is low and germination is variable, one could test the hypothesis that *C. hydrophilum* var. *hydrophilum* population itself is limited by seed production and/

or germination. A manipulative field experiment (+/– seed addition, crossed with soil disturbance and vegetation clipping treatments) with monitoring of germination and seedling survival over time would indicate the relative importance of these limitations.

A second hypothesis is that low genetic diversity correlates to low seed germination and/ or seed set. This could be tested by determining heterozygosity, alleles per locus, and inbreeding coefficients for various in *C. hydrophilum* var. *hydrophilum* patches and correlating these measures to site-specific patch size and reproductive output data (Hevroy et al. 2017; Shiga et al. 2017; Smith and Kay 2018).

Finally, as *L. haemorrhoidale* has not been studied in the context of conservation biology, one could test the hypothesis that the local abundance of other Cardueae correlates with presence of this seed predator in *C. hydrophilum* var. *hydrophilum*. Host choice experiments could test whether *L. haemorrhoidale* ovipositing females prefer *Centaurea solstitialis*, *C. hydrophilum* var. *hydrophilum*, or other Cardueae found in and around Suisun Marsh. Small scale, experimental removal of *C. solstitialis* could be conducted to investigate if predation on *C. hydrophilum* var. *hydrophilum* increases. Depending on the outcome of these experiments, management to reduce *C. solstitialis* in the vicinity of current or future restored populations of *C. hydrophilum* var. *hydrophilum* could be a forthcoming recommendation.

Because of reduced habitat, and by extension reduced geographic range, investigating and managing limiting life history stages is key to the persistence of this rare taxon and others in the California flora. Though generalizing across all rare species is impossible, it may be that other narrow endemic *Cirsium* taxa are limited by low seed set, high seed predation, limited localized dispersal, and/or low germination in small patches, given these taxa's similar phylogenies, life histories, and anthropogenic reduction of habitat and geographic range. With the exception of *C. fontinale* var. *campylon* (Hillman 2007), these life history constraints have not been comprehensively studied. Such investigations would improve conservation possibilities for these taxa, and inform the extent to which we can generalize about limitations and conservation strategies for this clade. Contrasting the rarest (i.e., listed) taxa with non-listed taxa may also provide insight into constraints associated with taxa limited to a few occurrences.

Particular attention is warranted for *C. hydrophilum* var. *hydrophilum* and other rare estuarine endemics with respect to climate change. In addition to changes in temperature, precipitation, and atmospheric carbon dioxide faced by all plants, new salinity and inundation regimes will also affect habitat quality and quantity for tidal wetland species (Parker and Boyer 2019), magnifying the importance of life history limitations, and perhaps directly impacting reproductive output. Species-specific knowledge of these limitations and how they relate

to environmental and habitat variables will increase effectiveness of management and conservation efforts.

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APPENDIX 1. SOIL MEASUREMENTS AND *CIRSIMUM HYDROPHILIUM* VAR. *HYDROPHILUM* DATA AT LOCATIONS USED TO QUANTIFY SEED SET IN 2012. N = five plants for inflorescence counts.

Site	Soil moisture, 0-2 cm (%)	Soil moisture, 2-6 cm (%)	Salinity, 0-2 cm (ppt)	Salinity, 2-6 cm (ppt)	Organic matter, 0-2 cm (%)	Organic matter, 2-6 cm (%)	# of plants	Mean # infl. per plant (SD)	Patch area (m ²)
E	79.2	78.3	46	36	62.5	47.1	10	8.6 (5.6)	8.3
F	80.9	82.1	35	39	55.1	47.9	69	21 (13)	96.3
G	81.2	79.5	19	20	57.7	47.6	21	111 (143)	25.8
H	65.2	61.8	15	15	33.2	28.1	26	51 (29)	63.0
I	81.5	78.4	37	30	48.6	38.1	113	52 (23)	235.8
J	68	70.3	14	12	35.4	34.0	62	59 (38)	48.1

A NEW SPECIES OF *HELIANTHUS* (ASTERACEAE) FROM CLARK COUNTY, NEVADA

TRENT M. DRAPER

4678 South 4075 West, Roy, UT 84067

trentdraper@hotmail.com

TODD C. ESQUE

United States Geological Survey, Western Ecological Research Center,
160 North Stephanie Street, Henderson, NV 89074

ABSTRACT

Helianthus devernii T.M.Draper is described as a new endemic species from two small desert spring populations found within Red Rock Canyon National Conservation Area, Clark County, NV. Morphological data and nuclear ribosomal ITS marker data place it in section *Ciliares* series *Pumili*. Furthermore, the molecular data allies it most closely to *H. pumilus* Nutt. *Helianthus devernii* differs from *H. pumilus* by its sessile one nerved opposite and alternate leaves, glabrous glaucous stems, and overall smaller heads. The two known populations of *H. devernii* of approximately 400 individuals occur near the Las Vegas Valley and are threatened by heavy recreational use and exotic plants and animals. A key to the species of *Helianthus* of Nevada is presented.

Key Words: Asteraceae, endemic, *Helianthus*, Nevada, new species, taxonomy.

A new species of *Helianthus* was first discovered serendipitously while conducting a botanical survey throughout the Spring Mountains, Nevada. The holotype was collected at an unnamed spring in Red Rock Canyon National Conservation Area (RRCNCA) in 2007. The first specimen collected had only the current year's inflorescence which was too young for identification. Nearly a month and a half later, the lead author returned to the spring and collected it in flower. Attempts at identifying the unknown "aster" were made using regional floras, but all identifications were unsatisfactory. The specimen was then brought to Professor Emeritus of Botany, Dr. Wesley E. Niles of University of Nevada, Las Vegas (UNLV), but Dr. Niles could not identify it to species with confidence. Dr. Niles then sent a specimen, collected subsequently by Dr. Patrick Leary of College of Southern Nevada, to Dr. Edward Schilling of the University of Tennessee. Dr. Schilling examined the specimen and stated that this find would be worthy of pursuing as a new species.

This new species of *Helianthus* is identified as belonging to section *Ciliares* series *Pumili* (Schilling and Heiser 1981). The morphological features along with the molecular data support this newly discovered *Helianthus* as a new species.

TAXONOMIC TREATMENT

Helianthus devernii T.M.Draper sp. nov. (Figs. 1, 2)
—TYPE: USA, NV, Clark Co. Red Rock Canyon National Conservation Area, unnamed spring, 22 July 2007, Draper 403 (Holotype: RENO105765; Isotypes: NY, ARIZ).

Helianthus devernii differs from other *Helianthus* in section *Ciliares* series *Pumili* by a combination of a

tufted, woody branched caudex; leaves one nerved, opposite and alternate, linear to narrowly elliptic, sessile, on glabrous and glaucous stems; with fewer and shorter ray flowers, and fewer disk flowers per head.

Perennial, tufted, herbaceous from a branched woody caudex, above ground portions dying back each year. **Stems** many, up to 1.02 m tall, glabrous, glaucous, previous year's stems usually present, turning bony white. **Leaves** cauline, sessile, one nerved (some lowermost weakly three veined), margins entire; proximal leaves opposite, lowermost usually deciduous at time of anthesis 40.6–56.3 mm long \times 4.4–9.0 mm wide; middle stem leaves largest 68.0–102.8 mm long \times 2.8–7.6(10.3) mm wide, linear-narrowly elliptic; distal leaves reduced upwards, alternate, linear 25.7–50.7(64.4) mm long \times 1.2–1.7 mm wide; abaxial and adaxial surfaces with multicellular strigose hairs and scattered spreading multicellular hairs, gland-dotted usually more so on abaxial side. **Heads** usually one per stem or stems, sometimes branched with one head terminating the branch. **Involucres** cylindric, 6.3–10.2 mm tall \times 5.6–6.3 mm wide. **Phyllaries** (2)3 series with multicellular, antrorse, hispidulous hairs, gland-dotted, apices acute, sometimes with a mucronate tip, 15–18 in number, ovate to lanceolate; outer 4.1–5.4 mm tall \times 2.0–2.5(3.5) mm wide; middle (6.1)6.9–7.2 mm tall \times (2.2)2.8–3.5 mm wide; inner (4.7)5.9–7.3 mm tall \times 1.6–2.7 mm wide. **Paleae** 7.8–8.5 mm, hispidulous distally, gland dotted, entire to rarely weakly three toothed-erose apically. **Ray florets** 5–8, laminae yellow, (7.3)9.0–10.7 mm long \times 3.8–5.0 mm wide, three toothed, abaxial side hispidulous, gland-dotted, sometimes with vestigial styles, adaxial side glabrous; sterile ovary as wide as ray tube, and smaller than fertile disk ovary. **Disk florets** 12–18(28), yellow;

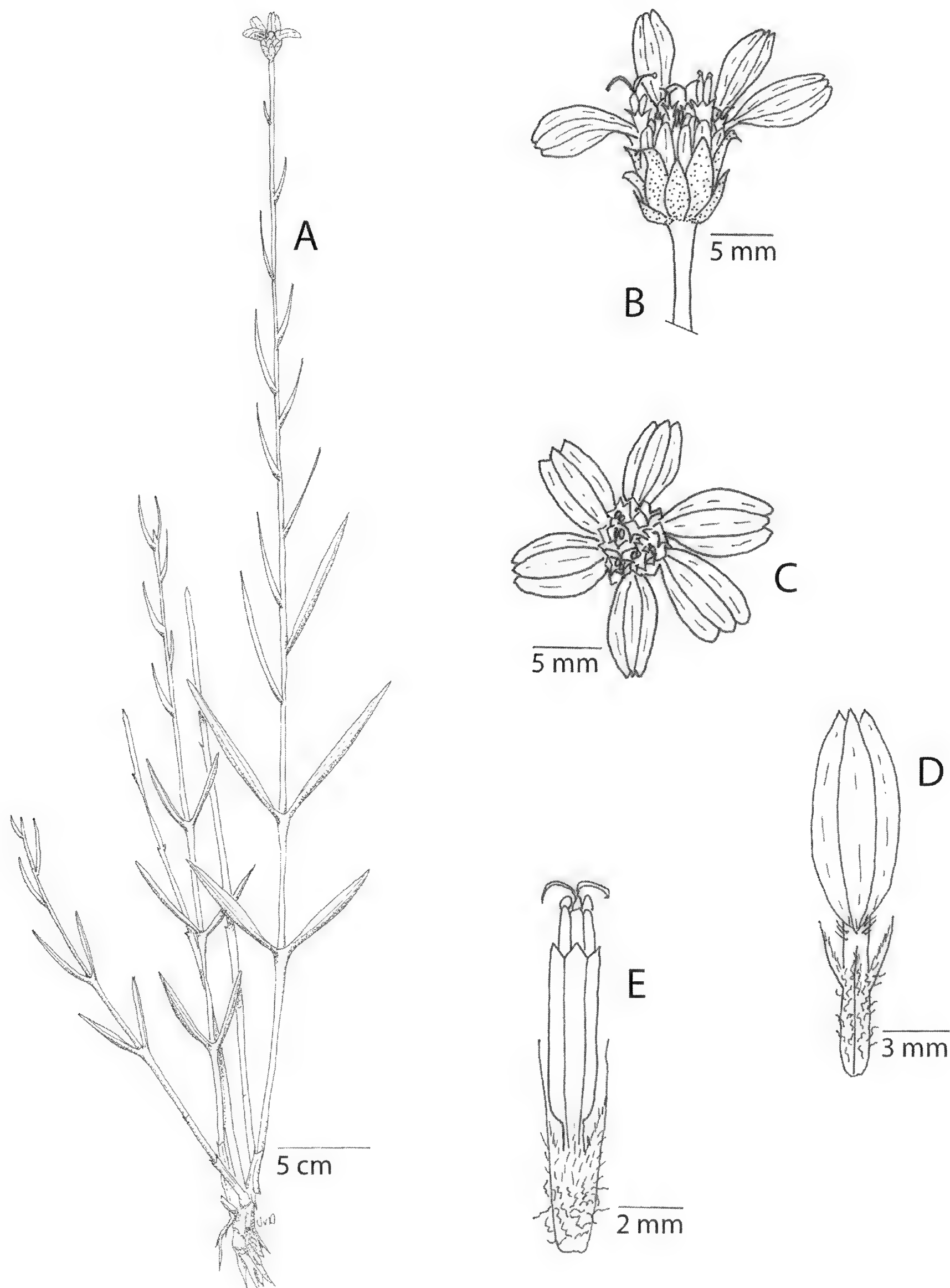


FIG. 1. Illustration of *Helianthus devernii*. A. Whole plant. B. Flower head. C. Top view flower head. D. Ray flower. E. Disk flower. Illustrated by Julie V. Draper from specimens collected from type location.

throat (4.5)4.7–6.2 mm long with multicellular hispidulous antrorse hairs, sometimes glandular especially proximally; tube abruptly constricted, 1.2–1.6 mm long, more or less glabrous. Anthers yellow when fresh, quickly turning brownish upon drying, with a few scattered, spreading hairs; appendages mostly yellow sometimes with some brown; stigmas hispidulous. **Cypselae** quadrangular, 3.5–4.0 mm long, tan with scattered brown specks, proximal end beset with tomentose hairs, soon deciduous, distal end with straight, ca 1.2 mm, erect/antrorse hirsute hairs; pappus of 2–3 deciduous awns/scales (lacerate/erose) sometimes with 1–4

shorter awn like setae (Figs. 1, 2). Note: measurements are from fresh material.

Paratypes: All from USA, Nevada, Clark Co., Red Rock Canyon National Conservation Area. 03 Aug 2019, Draper 686 (TENN, UTC); 03 Aug 2019, Draper 687 (RENO, NY); 25 Aug 2007, Leary and Landau 6609 (RENO, NY).

PHENOLOGY

Helianthus devernii starts growing from the basal caudex in March and flowers from June through September.



FIG. 2. *Helianthus devernii*. A. Whole plant. B. Flower head. C. Side view of flower head. D. Middle cauline leaf. E. Stem and lower leaf attachment. F. Habitat.

DISTRIBUTION AND HABITAT

Helianthus devernii is distributed on lands administered by the U.S. Department of the Interior, Bureau of Land Management (BLM) and within the RRCNCA at the eastern base of the Spring Mountains, Clark County, Nevada, and private land holdings within the RRCNCA. The Spring Moun-

tains were previously home to 13 endemic taxa of plants (Niles and Leary 2007). The 14th endemic, *Helianthus devernii*, has only been found at two springs within the RRCNCA. The two populations are growing in a desert spring community associated with moist soils of red sandstone alluvium (from Aztec sandstone) (Page et al. 2005), and often with a thin layer of saline crust. The desert spring vegetative

TABLE 1. Comparison of 15 characteristics in seven perennial species of *Helianthus* section *Ciliares* (Heiser et al. 1969; Schilling 2006). ¹ Series *Pumili*.

Characteristic	<i>H. devernii</i> ¹	<i>H. arizonensis</i> R.C.Jacks	<i>H. ciliaris</i> D.C.	<i>H. cusickii</i> ¹	<i>H. gracilentus</i> ¹	<i>H. laciniatus</i> A.Gray	<i>H. pumilus</i> ¹
Habit	tufted	creeping roots	rhizome, creeping roots	taproot	taproot	creeping roots	taproot
Stem	glabrous, glaucous	glabrous, glaucous	glabrous, glaucous	glabrous, glabrate	hairy	hairy-glabrate	hairy
Leaf arrangement	opposite to alternate	opposite	mostly opposite	mostly opposite	mostly opposite	opposite to alternate	opposite
Leaf attachment	sessile	sessile	sessile	sessile to petiolate	sessile to petiolate	sessile	petiolate
Leaf shape	linear to narrowly elliptic	lanceolate	linear to lanceolate	lance-linear to lanceolate	lanceolate to lance-ovate	lanceolate	lanceolate to ovate
Leaf nerves	1	1-3	1-3	3	1-3	1-3	3
Leaf surfaces	glandular	non-glandular	non-glandular	glandular	glandular	glandular	glandular
Involucre diameter mm	5.6-6.3	9-18	12-25	12-28	13-20	10-24	7-14
Ray laminae	glandular	non-glandular	non-glandular	glandular	glandular	non-glandular	glandular
Phyllary surfaces	glandular	sparingly glandular	non-glandular	glandular	glandular	glandular	glandular
Disk Color	yellow	yellow	red	yellow	red	red	yellow
Anther color	yellow	reddish brown	brownish red	orange brown	reddish brown	purple	dark brown
# of disk flowers	12-18(28)	>30	>35	>40	>50	>40	>30
# of rays flowers	5-8	10-14	10-18	12-16	13-21	14-20	8-13
Ray length mm	(7.3)9.0-10.7	7-9	8-9	20-35	15-25	8-11	15-20

communities consist of *Fraxinus velutina* Torr., *Cirsium mohavense* (Greene) Petr., *Sporobolus airoides* (Torr.) Torr., *Sporobolus compositus* (Poir.) Merr., *Muhlenbergia rigens* (Benth.) Hitchc., as well as some plant taxa associated more with upland habitats such as *Amsonia tomentosa* Torr. & Frém., *Heterotheca villosa* (Pursh) Shinnery var. *scabra* (Eastw.) Semple, and *Gutierrezia microcephala* (DC.) A.Gray. The *H. devernii* population at the first spring covers about 800 square m with less than 100 individuals estimated and the population at the second spring covers about 1800 square m with less than 300 individuals. The vegetative community separating the two springs and *Helianthus* populations is a mixed desert shrub community of *Coleogyne ramosissima* Torr. and *Ambrosia dumosa* (A.Gray) W.W.Payne with the exotic *Bromus rubens* L. in the shrub interspace.

Trails and old dirt roads traverse through the two populations of plants. Near one of the springs, a water well head (unknown if it is active) is present within the population of *H. devernii*.

Two additional springs within the area lie to the north and south of the *H. devernii* populations respectively. No populations of *H. devernii* have been found at these springs.

TAXONOMIC CONSIDERATIONS

The majority of perennial species of *Helianthus* in the western United States belong to section *Ciliares* (Heiser et al. 1969). *Helianthus devernii* belongs to section *Ciliares* as identified by the key in Schilling and Heiser (1981). Placement into series is more difficult. As stated by Schilling and Heiser (1981) series *Ciliares* has slender roots, sessile leaves, glabrous phyllaries and stems usually glaucous, versus series *Pumili* with stout roots, some leaves petiolate, phyllaries usually pubescent and stems not glaucous. *Helianthus devernii* meets two of the four criteria for each series. Molecular analysis of the nuclear ribosomal internal transcribed spacer (ITS) sequence (Genbank MN414466) generously performed and provided by Dr. Edward Schilling of the University of Tennessee (personal communication) concluded that *H. devernii* is not only unique but is most closely allied to *H. pumilus* Nutt. of series *Pumili*. Additionally, series *Pumili* has gland-dotted leaves, phyllaries and abaxial ray laminae. Series *Ciliares* does not have gland-dotted features in any combination of characteristics. *Helianthus devernii* has gland-dotted leaves, phyllaries, and abaxial ray laminae. Therefore *H. devernii* is placed in series *Pumili* alongside *H. cusickii* A.Gray, *H. gracilentus* A.Gray and *H. pumilus*.

Helianthus gracilentus occurs in western California south into northern Baja California, Mexico. *Helianthus cusickii* occurs in northern California, northwestern Nevada, Idaho, Oregon and Washington. *Helianthus pumilus* is found in Colorado and Wyoming. Compared to *H. devernii*, all three of the above taxa are taprooted, with leaves one to three

veined, mostly opposite and overall wider on glabrous to hairy stems; with larger number and length of ray flowers, and more numerous disk flowers per head (Schilling 2006). In contrast, *H. devernii* is only found in southern Nevada; has a tufted, woody branched caudex; leaves one nerved, opposite and alternate, linear to narrowly elliptic, sessile, on glabrous and glaucous stems; with fewer and shorter ray flowers, and fewer disk flowers per head than the others in series *Pumili* (Table 1).

CONSERVATION STATUS

We suggest to the Nevada Division of Natural Heritage and the Nevada Native Plant Society to study the conservation status of *H. devernii* at their annual rare plant meeting. Despite the inclusion of some of the population of *H. devernii* residing within the Bureau of Land Management’s protected boundaries of the RRCNCA, heavy recreational use, burro (*Equus asinus* L.) disturbance, any over-pumping of ground water, and fires fueled by exotic grasses (i.e., *Bromus rubens*) are presumed threats to the two small populations of less than 400 individuals.

ETYMOLOGY

The specific epithet of “devernii” honors the lead author’s grandfather, DeVern Campkin, who encouraged and fostered a love in science, history and geography. He always had a book or map to study and look at or an answer to a question the author had as a child in the days before the age of the Internet. A suggested common name is Red Rock Sunflower in honor of Red Rock Canyon National Conservation Area.

KEY TO THE *HELIANTHUS* SPECIES OF NEVADA
(ADAPTED FROM HEISER ET AL. 1969; SCHILLING 2006)

- 1. Plants perennial
 - 2. Leaves sessile
 - 3. Leaves 3 nerved; ray laminae > 20 mm long *H. cusickii*
 - 3’ Leaves 1 nerved; ray laminae < 11 mm long *H. devernii*
 - 2’ Leaves petiolate
 - 4. Phyllaries not gland-dotted
H. nuttallii Torr. & A. Gray subsp. *nuttallii*
 - 4’ Phyllaries gland-dotted
 - 5. Stems glabrous; abaxial ray laminae gland-dotted; native species in northwestern Nevada *H. cusickii*
 - 5’ Stems hairy; abaxial ray laminae not gland dotted; waif species, may not persist
. *H. tuberosus* L.
- 1’ Plants annual
 - 6. Phyllaries ovate with the distal half abruptly contracted into a long acuminate tip *H. annuus* L.
 - 6’ Phyllaries linear to lanceolate, not suddenly contracted into an acuminate tip

- 7. Leaves, abaxial ray laminae and phyllaries gland dotted
. *H. deserticola* Heiser
- 7’ Leaves, abaxial ray laminae and phyllaries not gland dotted
 - 8. Stem with some hispid hairs; heads usually with a subtending bract; phyllaries 2–3.5 mm wide.
H. petiolaris Nutt. subsp. *fallax* Heiser
 - 8’ Stem usually hispidulous to strigillose; heads usually without subtending bracts; phyllaries 3–5 mm wide
. *H. petiolaris* subsp. *petiolaris*

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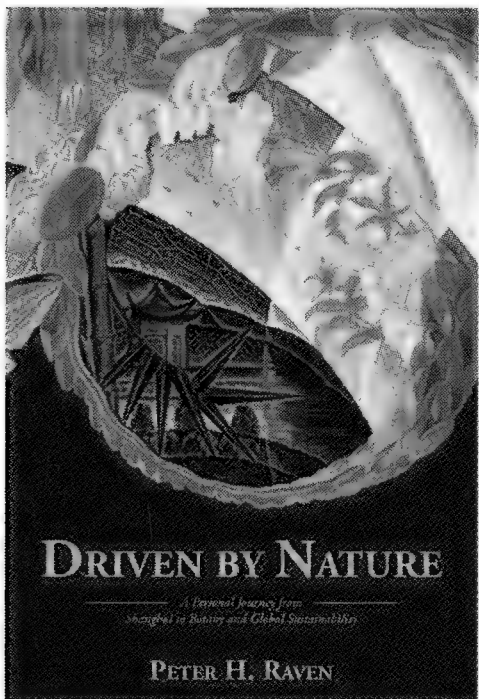
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Review



Driven by nature: A personal journey from Shanghai to botany and global sustainability. By Peter H. Raven. Missouri Botanical Garden Press, Saint Louis, MO. 408 pp. ISBN 9 78-1935641193 (hardcover). Price \$35.00.

Driven by Nature is the aptly titled, beautifully written, and inspirational story of the evolution of a precocious boy fascinated by insects and plants, who progressively became a prominent academic scholar, an enlightened administrator, a national/international science policy maker, and a highly effective advocate for the preservation of life on Earth. Set against the background of family perturbations, major scientific discoveries, and cultural/social/political events of the past 85 years, Peter Raven's autobiography delivers both historical perspective and thought-provoking reading. The story begins with Raven's ancestors and their arrivals in California, fortunes and losses in China, and a boyhood spent discovering nature in the Bay Area and Sierra Nevada. It combines moving and eventful episodes (e.g., the Donner Party's perilous crossing of the Sierra Nevada in 1846–1847, on which his great-grandfather's family nearly starved and froze to death, but survived thanks to a compassionate volunteer rescuer) with amusing personal anecdotes (e.g., the 13 year-old nature nerd, being informed of the facts of life in terms of mating insects from the Chinese obstetrician who had delivered him in Shanghai). Raven describes the early shift in his focus on nature's creatures thusly: "At eleven, flowers were places where I could often find beetles; at twelve, I brushed beetles off to get to the plants on which they had gathered!" His interest in insects and plants was nurtured at the student section of the California Academy of Sciences, and subsequently in that institution's research departments. Alice Eastwood and Tom Howell, curators of botany, became his early botanical mentors. He collected plants (rediscovering two in San Francisco that were subsequently described as new species) for and became a coauthor of *A Flora of San Francisco, California* in 1958. Insightful discussions about other important mentors during his times as a naturalist on Sierra Club Base Camp outings, and as a student at

college (UC-Berkeley) and graduate school (UCLA) include such 20th century botanical luminaries as Ledyard Stebbins, Lincoln Constance, Herbert Mason, Mildred Mathias, and Harlan Lewis. It was during his graduate work that the evening primrose family (Onagraceae) became the focus of Raven's botanical pursuits. Joining the biology faculty at Stanford in 1962, Raven and Paul Ehrlich became friends and collaborators working with butterflies and plants. Indeed, their development of the concept of coevolution and studies thereon altered the face of evolutionary biology. While at Stanford, Raven explains a broadening of his interests, research activities, and personal relationships as someone coming to terms with scientific breakthroughs and cultural changes during the second half of the 20th century. This led to a major "reset" from his focus on generating basic scientific knowledge to using that knowledge to understand broader environmental implications—from his days of intensive plant collecting to more theoretical and practical applications ("population growth, biological extinction, and sustainability")—resulting in an intense conservation ethic.

Raven desired to bring people together to accomplish important things for humans and for the biosphere they share with other living creatures. Perhaps more than any other botanist, he has succeeded in those efforts, and we all share the benefits of those successes. An affinity for people and encouraging collaboration are shown to be keys to much of Raven's productivity and influence. His philosophy on successful leadership was put to the test when he became director of a multi-faceted organization, the Missouri Botanical Garden. During nearly 40 years there, he transformed an important but underutilized and underdeveloped botanical garden into a global center of botanical research, horticultural excellence, and education at every level—an asset with resources, influence, and importance unmatched in the Americas. At the Garden and on myriad national and international committees, councils, and panels on which he has served, Raven was able to build on his earlier experiences: from watching butterflies collect plant nectar as a child, to co-founding the discipline of coevolution by studying plant/butterfly interactions with Ehrlich, to adding a butterfly house to the Garden's facilities; from producing local floras in his student days to his subsequent planning/organizing of major international floristic efforts (e.g., China, Mesoamerica, North America); and from seeking funding for his own scientific studies to garnering funds for science, scientific infrastructure, and scientists in countries around the globe in desperate need of support.

Raven's accomplishments and subsequent standing in the scientific and conservation communities gave him access to prominent politicians and wealthy individuals. He used his unparalleled international influence toward the pursuit of biological surveys and conservation of natural resources to build collaborative scientific bridges between nations, including former U.S. political foes (e.g., China, Japan, Nicaragua, Soviet Union/Russia, and Vietnam). Becoming the most respected, awarded, and influential botanist of his generation did not come without costs, and Raven does not shy away from analyzing and critiquing his personal life, both its successes and failures. A demanding work-ethic was essential to his career and accomplishments, but was not always conducive to a stable family life. Nevertheless, the importance and support of his extended family is palpable in compassionate and interesting discussions throughout the narrative.

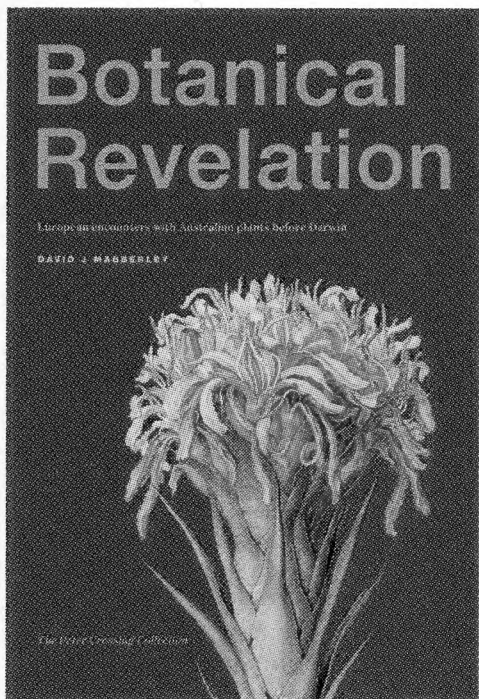
Some who become leaders perform (often admirably) the duties proscribed. Others go beyond that and seek new challenges, create new opportunities for staff/members/constituents, increase funding and sources thereof, encourage collaboration, and make new disciplinary and/or societal connections. There are few better role models of the latter type of leader than Peter Raven. The insights offered in his autobiography provide a model for anyone purporting to become the kind of successful and inspiring leader who truly makes a difference. He became a self-described "global evangelist for sustainability and conservation" via the lecture circuit, publica-

tions, and international meetings/conferences. Yet, for all of the accomplishments Raven recognizes that credit for them lies largely with the staff, collaborators, friends, funders, supporters, and beneficiaries—working together toward a common goal of sustaining life on our fragile planet.

Ultimately, *Driven by Nature* is the intimate story of the author's personal journey from discovering, describing, and understanding the Earth's biodiversity to concerted efforts to preserve it for future generations amid its rapidly increasing destruction caused by one of its species. This comes with the ironic recognition that it is this very biodiversity and its interconnectedness, the web of life, on which that species also depends for its own survival. The book features a cogent and thoughtful epilogue stating the issues and challenges of this critical message—"a world already living on an acute ecological deficit." It concludes with a call to action—to seek our better nature, to acknowledge and cooperate in addressing the complex environmental issues now threatening the peace and stability of the planet on which all life depends. Raven asserts that the necessary "change" called for in peoples' thinking and the actions needed to meet these challenges begins with self-examination. This book does that willingly and eloquently for Peter Raven; and it provides so much more for those who read it!

—THOMAS F. DANIEL, Curator Emeritus, Botany, California Academy of Sciences, San Francisco, CA 94118.

Review



Botanical revelation: European encounters with Australian plants before Darwin. By D. J. MABBERLEY. 2020. NewSouth Books, University of New South Wales, Sydney, Australia. 384 pp. ISBN 978-1742236476 (hardcover). Price \$89.99.

David J. Mabberley, in his new tome, *Botanical Revelation: European encounters with Australian plants before Darwin*, thoroughly examines this fascinating period of time in botanical history with the accompaniment of numerous remarkable drawings and prints of original texts never before shared with the public. The cover of this stunning work is a beautiful reproduction of a *Doryanthes excelsa* Corrêa (Gynea Lily) engraving by Ferdinand Bauer from 1826, with the inside of the jacket revealing an intriguing 19th-century map of New South Wales and the Australian continent. This book is an indispensable addition to any professional library or serious collector of botanical books.

Botanical Revelation is the result of comprehensive and detailed research, as seen in the heavily referenced text. Using historical accounts, primary literature, illustrations, and herbarium specimens found in the Peter Crossing Library, Mabberley presents a history of the Australian flora in a new way, illuminating the interplay between European exploration and fascination with Australian plants and its inevitable influence on European gardens, art, and economics pre-Darwin.

In chronological order starting with the first Australian plant record from 1606, Mabberley outlines a rich history of those who journeyed to Australia (from the well known to the obscure), the voyage route and details, what the explorers, scientists, and others learned from their experiences, and the influences on culture and science once the discoveries were disseminated across Europe. Paralleling these captivating histories is a thorough historical treatise on European botanical artists and

gardeners, an illuminating art form of its own that is oftentimes overlooked.

Mabberley's inclusion of historical context, such as stating that Bruni D'Entrecasteaux reached Tasmania two days before Louis XVI was executed and that the king was said to have inquired about news of the voyage on his way to the guillotine, as well as other intriguing facts, adds to the readability of the narrative. Through such anecdotes, he shows how flora brought Australia to the forefront of global significance at a time when Europe dominated.

Describing the rise of nurseries and botanical periodicals, *Botanical Revelation* details lines from original text such as William Townsend Aiton's 1814 *Epitome of the second edition of Hortus Kewensis* (that Mabberley describes as "oily"), stating the printing of this information as "necessary to the public" and that the patronage of the king "has rendered Botany a favourite pursuit among all the classes of Your Majesty's people." By sharing this historical perspective, Mabberley helps the reader gain a sense of the political and social climate in which these events occurred. Interspersed into this robust narrative are comprehensive sidebars highlighting specific Australian plant species, typically including vibrantly colored illustrations or engravings, ethnobotanical information, and either the history of their European discovery or other compelling facts about the species' spread to the greenhouses and gardens of Europe.

Mabberley's extensive background affords him the expertise and knowledge to create this impressive book, successfully illustrating connections between art, history, philosophy, natural science, and culture. He ends the book by putting forth the mysteries yet to be discovered in the floristic world, in Australia and elsewhere, and writes of the significance of botanical illustration in documenting diversity as well as the importance of curiosity and continued exploration.

If you are intrigued by Australian plants, beautiful botanical art, the history of flora, scientific discovery, the economic implications of plants throughout the eras, or the history behind Darwin's theory of evolution in intricate detail, then you will find a gem in *Botanical Revelation*.

—DENA PAOLILLI AND MATT RITTER, Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407.

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